Sveriges lantbruksuniversitet
Swedish University of Agricultural Sciences

Faculty of Natural Resources and
Agricultural Sciences (NJ)

Effects of global warming on Eurasian perch (*Perca fluviatilis*) in the Baltic Sea

- Does the growth response to increased temperatures differ along a latitudinal gradient?

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Department of Aquatic Resources
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- Does the growth response to increased temperatures differ along a latitudinal gradient?

Effekter av global uppvärming på abborre (*Perca fluviatilis*) i Östersjön
- Förändras tillväxtresponsen på en ökad temperatur längs en latitudinal gradient?

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Abstract

Anthropogenically caused climate change, i.e. global warming, is anticipated to affect all living organisms. Particularly ectotherms are predicted to show strong responses to the increased warming, as their body temperature closely tracks ambient temperatures and because body temperature profoundly affects many physiological functions e.g. locomotion, fecundity, metabolism and growth. This study attempts to answer whether increasing temperature has affected the growth rate and body length at age in Baltic Sea perch, and if the effect of increasing temperatures varies depending on latitude.

It was carried out through analyses of temporal trends in size-specific growth at different ages (growth years), size-specific growth rates estimated from the whole life-span, as well as length at age one in perch from three areas in the southern (Kvädöfjärden), central (Finbo) and northern (Holmön) Baltic Sea, and by analysing whether variation in temperature explained the observed changes over time. Positive relationships were found between body length at age one and temperature in all areas. Size-specific growth rate at age increased significantly with temperature, for all ages and locations, except for six-year old perch in Holmön. All size classes of Finbo and the 145 mm class of Holmön and Kvädöfjärden demonstrated positive relationship of the size-specific life-span integrated growth rate with increasing temperatures, but the smallest and largest size classes in those two areas did not. Of the three areas investigated, my results suggest that the responses in body length at age one and size-specific growth rate for growth year one and two to increased temperature were comparatively stronger in the north than in the central and south Baltic Sea. For the size-specific growth of older individuals or in the size class 145 mm, no such latitudinal pattern emerged.

Overall, adjusted r^2 values were low, indicating that temperature does not explain the variation in growth rate well for any of the models. Still, the significant relationships to temperature indicate that warming could have contributed to increased perch growth rate and temperature, and that the response in growth for individuals younger than three years old, has been strongest in the north. This knowledge may be useful when making predictions on how an additional increase in temperature may affect the growth, and body length of perch. It may also help to generate a broader understanding of how the perch growth response changes to increasing temperature, given different latitudinal distributions.

Keywords: body-length at age, size dependent growth, *Perca fluviatilis*, climate change, temperature, Baltic Sea, latitude

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Introduction

Anthropogenic climate change is predicted to have major, irreversible effects on ecosystems globally. Thus far, three major responses have been documented in natural systems: shifts in species' distribution range (Cheung et al. 2010), change in phenology (Walther 2010) and declining body sizes (Daufresne et al. 2009). Ectothermic species constitutes the clear majority of all known species – roughly 99% of all known species (Atkinson & Sibly 1997). The body temperature of ectotherms closely follows that of the surrounding temperature. They are therefore predicted to show strong responses to climate warming, as the rate of biochemical reactions, vital to energetic processes such as metabolism, are strongly temperature-dependent (Hochachka et al. 2002; Angilletta 2009).

The common phenotypic response of reduced final body size in ectotherms to warming can be described by the temperature size-rule (TSR) (Atkinson 1994). The TSR states that higher temperatures during ontogeny leads to a quicker development (from egg to adult) and growth rate (increase of somatic mass) in juveniles, while causing a decline in adult body size (Atkinson 1994). This results in a shift in body size at age or life stage, which is determined by the temperature dependence of development and the growth (Berrigan & Charnov 1994). However, the response in final body size is further influenced by factors other than temperature, e.g. Hoefnagel & Verberk (2015) found the "classic" TSR response in hypoxic conditions only, and the reversed TSR (higher rearing temperature and larger final body-size) in hyperoxic settings when comparing individuals of an aquatic crustacean species reared under different temperature and oxygen conditions.

In marine and aquatic systems, oxygen supply is an important determinant of thermal tolerance and performance of ectotherms (Pörtner 2002; Stevens et al. 2010) which in combination with food and temperature influences the final body-size (Hoefnagel & Verberk 2015). Higher temperatures will increase the rate by which biochemical processes occur. This increases the growth potential (Ohlberger 2013; Gillooly et al. 2001), but also the oxygen demand of the individuals, while decreasing the oxygen solubility of the water (Pörtner & Knust 2007). Such a mismatch between oxygen supply and demand could reduce the thermal tolerance and growth of the individual (Cheung et al. 2013). As the oxygen uptake is related to the respiratory surface of the individual, it scales allometrically, whereas the cost of maintenance scale isometrically with body size as it depend on body size (Von Bertalanffy 1957), any imbalance between oxygen demand and oxygen dissolved in the water will thus be further amplified as size increase (Pörtner & Knust 2007).

Body size differs with latitude and two contrasting patterns with respect to latitudinal differences can be distinguished. First, body size increase with latitude (decreasing temperatures), which is usually attributed to the negative relationship of body size and rearing temperature (Atkinson 1994; Ernsting & Isaaks 1997; Blanckenhorn & Hellriegel 2002), and is seen in e.g. populations of Eurasian perch (*Perca flutiatilis*), as shown by Heibo et al. (2005). Secondly, a decrease in body size with latitude, which is suggested to be connected to generation time, the length of the season and ultimately resource constraints (Nylin & Gotthard 1998; Roff 1980). Further, certain populations of terrestrial insects have been found to display a pattern of larger adult body sizes at increasingly lower altitudes (increasing temperatures) (Chown & Klok 2003) in an area were seasonality has a major influence on resource availability. This pattern may be ascribed to several different mechanisms, e.g. selection of larger sized individuals in order to ensure survival over winter or prolonged periods of resource shortage (Chown & Klok 2003) or that the varying sensitivity in growth and development to temperature affects the increase in body size (Van Der Have & De Jong 1996).

Assuming that food and oxygen are not limiting for growth, warming increases growth rate for small as well as large individuals given that ambient temperatures are below optimum for growth (Hoefnagel &

Verberk 2015). The optimal temperature (T_{opt}) for growth varies between species, between individuals of the same species and generally decreases as body size increases (Björnsson & Steinarsson 2002). Warming beyond T_{opt} may cause enzyme systems to break down and result in an increased mortality rate and possibly a complete loss in abundance, which would affect larger individuals first (Pörtner & Knust 2007), due to their generally lower T_{opt}. Species that are fairly related and reside in the same area can display different responses towards increased temperature (O'Gorman et al. 2012), which may be explained by differences in T_{opt} between the species. It is further plausible that different populations of a species, who may share the same T_{opt} for growth, display different responses towards increasing temperature in areas of different latitudes as the ambient temperature (T_{hab}) may differ. Deutsch et al. (2008) demonstrated that the critical maximum temperature (CT_{max}) in terrestrial ectotherms, i.e. insects, decreased less rapidly with latitude than air temperatures, resulting in a higher warming tolerance for insects living at higher latitudes. Moreover, at low latitudes, where T_{hab} is higher, insects are living closer to their physiological optimum, than compared to higher latitudes. Thus, insects at high latitudes, compared to those at low latitudes, have a broader thermal safety margin (TSM), which is defined by the T_{opt} relative to T_{hab} (Deutsch et al. 2008). Although terrestrial and aquatic ectotherms live in distinctively different environments, their thermal biology may still be similar. As such, it may be suggested that marine and terrestrial ectotherms may display similar patterns of higher warming tolerance with increasing latitude (Compton et al. 2007). Because of the broader TSM, it is further reasonable to suggest that any positive response to warming may be stronger in populations at high latitudes than at low latitudes. However, if the T_{opt} for growth is different between the populations due to local adaptions, and the TSM remain the same between the populations, it may be suggested that similar responses towards temperature increase is to be expected.

Baudron et al. (2014) investigated changes in body size for eight commercially fished species between 1970 and 2010, and found that six of eight species underwent synchronous reductions in body size coinciding with a temperature increase in the North Sea. Rindorf et al. (2008), performed analyses on North Sea cod caught between 1983 and 2006, and found that temperature and growth of young cod correlate positively, though without translating into increased body length at age one. Further, though growth of juveniles correlated strongly with ambient temperatures, no indication of temperature limitation on older cod were found, which is consistent to findings of Righton et al. (2010). Thresher et al. (2007), analysed long-term (1871 to 1992) time series of reconstructed growth data from otoliths and found that six out of eight commercial exploited species showed significant changes in growth rate over time. The response in growth differed depending on depth such that increasing temperatures near the surface decreased the growth rate of deep-water species, while increased the growth rate of species living closer to the surface. Whether latitudinal differences in distribution of a species can mediate the species response to warming, as would be predicted given similar thermal adaptations but in different thermal environments, has not been assessed in natural systems.

In this study, time series of back-calculated length at age estimates of Eurasian perch (*Perca fluviatilis*) (henceforth only perch) were used to assess how temperature has affected growth and body length of perch in populations along a latitudinal gradient in the Baltic Sea, one of the fastest warming oceans globally with an annual increase in temperature of 0.054°C between 1982 and 2006 (Belkin 2009).

The following hypotheses were tested:

1. Increased temperatures have increased the body length at age one in all areas.
2. Increased temperatures have increased the size-specific growth rate of all ages and sizes of Baltic Sea perch in all areas, assuming that food and oxygen has not been limiting for growth.

3. The growth response to increased temperature increases with latitude (i.e. is strongest in following order: northern, central and southern Baltic Sea), given that the TSM (thermal safety margin) becomes broader with latitude and that all populations roughly share the same T_{opt} for growth.

Materials and Method

Study species

Perch is an iteroparous species, common in fresh- and brackish waters throughout Europe. Perch spawn in nearshore areas in February to July depending on the latitude, though usually when water temperatures approach 6°C (Freyhof & Kottelat 2008). Young of the year (YOY) perch feed on zooplankton the first weeks of life. As zooplankton density decreases towards the end of summer, the YOY perch may switch to include macroinvertebrates in their diet (Heibo et al. 2005). They may then undergo another ontogenetic diet shift from benthivory to piscivory, which is usually accompanied by increased growth rates (Heibo et al. 2005). Female perch generally mature at the age of three to five years, at the length of approximately 150 to 180 mm, while male perch usually mature at the length of 100 to 120 mm at an age of two to three (Heibo et al. 2005; Danielsson 2007), however, only female perch were used in this study. Perch is further considered both euryhaline and eurythermal, meaning it is tolerant to a wide range of temperatures and salinities (Lehtonen 1996; Sperandio 2013).

Study areas

The perch used in my analyses were caught in three areas of different latitudes in the Baltic Sea, Holmön at 63° N (20° E), Finbo at 60° N (19° E) and Kvädöfjärden at 58° N (16° E).

Temperature data

Temperature data for the study period (1970-2016) were acquired from the ICES Oceanography database (http://ocean.ices.dk/HydChem/HydChem.aspx), in which data collected on national level is compiled. Observations consisted of both high resolution CTD and bottle data. For each location, mean temperatures in August were used as a proxy for the annual sea surface temperatures (hereafter SST) to ensure large enough sample size to calculate representative means and to ensure that the timing of sampling did not vary between years, which could bias the temporal trends. Further, as temperature samples were derived from different depths in the water column, only data from depths <10 meters were used to reduce potential bias (see Table A6 in the Appendix). In total, 2879 temperature observations were used (762 for Holmön, 1660 for Finbo and 801 for Kvädöfjärden). The locations of the temperature samples are seen in Figure 1. The collated temperature data were compared to the in-situ data collected during the fishing to test for similar temporal trends (see Figures A1, A2 and A3 in the Appendix). The in situ measured temperatures and the ICES temperature data demonstrated similar trends in all areas. In Holmön, in the period 1989 to 2016, the in-situ measured temperature demonstrated an increase in temperature of 0.037 [°C $Year^{-1}$], while the ICES data demonstrated an increase of 0.042 [°C $Year^{-1}$]. In the period 1976 to 2016 in Finbo, the in-situ measured temperature increased with 0.15 [°C $Year^{-1}$], while the ICES data demonstrated an increase of 0.067 [°C $Year^{-1}$]. In Kvädöfjärden, ICES and in-situ measured temperatures were compared in the periods of 1962 to 1972, and 2001 to 2016. The in-situ measured temperatures demonstrated an increase in temperature of 0.11 [°C $Year^{-1}$], while the ICES temperature demonstrated an increase of 0.06 [°C $Year^{-1}$]. As the effects were similar and because the ICES data provided longer series on temperature for all areas, with fewer years missing, this was the

data used. The collated time series of SST for each location was in the same order of magnitude as has been reported for the Baltic Sea in total (Belkin, 2009), and the August temperature used was correlated to the variation in annual mean temperature for the whole growth season, May-September (Figure A4). For Holmön, there was no temperature data for the years 1971, 1972 and 1982 and for Finbo, there was no temperature data for 1982.

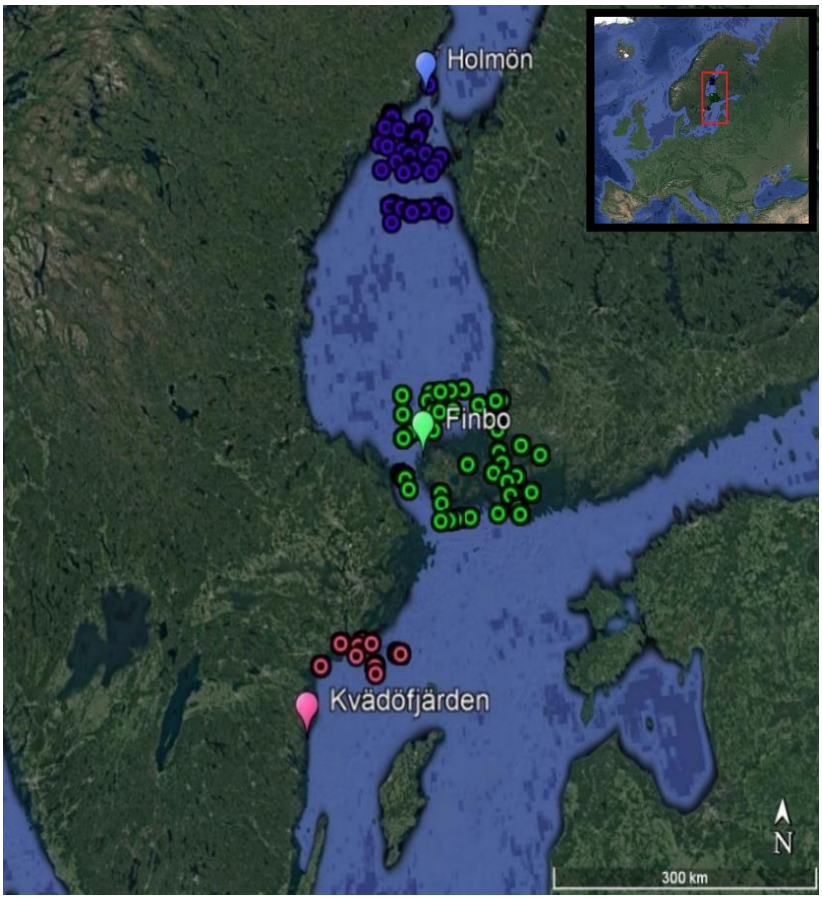

Figure 1. Spatial distribution of the ICES sea surface temperature observations used for the study areas.

Fish sampling

Different types of fishing gear where used for the fish sampling in the different areas and time periods. Survey-gillnets ("kustöversiktsnät") were used between 1977 and 2003 for Holmön, and between 1988 and 2002 for Finbo. Nordic survey-gillnets ("Nordiska kustöversiktsnät" described in European Standard EN 14757:2005) have been in use in both areas since 2003 (Andersson 2009). The shift from survey-gillnets to Nordic survey-gillnets may have affected the analyses of Finbo and Holmön. The final length of perch in a 10-year period before and after 2002 were compared for ages 1 to 6, and some differences between these two periods were detected. E.g. very few or none, one-year-old perch were caught in the 10-year period before 2002, compared to the 10-year period after 2002 (see Figures A5 and A6 in the Appendix), as expected due to the smaller mesh size included in the range of mesh sizes of Nordic survey-gillnets. Gillnets ("Biologiska länkar") were used in Kvädöfjärden between 1971 and 1988 and gillnets of the type ("Nätlänkar") have been in use from 1989 to present. The effect of the fishing gear shift in Kvädöfjärden was investigated by comparing the final length of caught perch of in the period 1978 to 1988, to the final length of perch caught between 1989 and 1999 for ages 1 to 6. No 1-year-old perch, and very few 2-year old perch were caught in the period 1978 to 1989, compared to the period 1989 to 1999 (see Figure A7 in the Appendix). All fishing took place in August annually, except for Kvädöfjärden, where fishing in the shallow water took place between July 25th and August

15th, and in the deep waters right after autumn circulation when bottom temperatures were less than 12°C. For all areas, nets were put in the water between 2-5 pm and collected the following day between 7-10 am (Söderberg 2008; Andersson 2009). The survey-gillnet is a three meters deep and 35 meters long bottom net that consists of five seven meters long parts with different mesh sizes (17, 22, 25, 33 and 50 mm). The Nordic survey-gillnet is 1.8 meters deep and 45 meter long, with a total area of 81 m^2. The nets are composed of nine, five meters long sections with different mesh sizes and provides a sample which is stratified in respect to depth. Gillnet ("Biologiska länkar") are 27 meters long, with mesh sizes ranging from 21.5 to 60 mm. When fishing with gillnet ("Nätlänk"), different mesh sizes were used depending on depth. Fishing in deep areas (14-20 meters), mesh sizes 21, 30, 38, 50 and 60 mm were used, while fishing in shallow areas (2-5 meters), mesh sizes 17, 21, 25 and 30 mm were used (Andersson 2009). The specifications of each fishing gear are compiled in Table A5 in the Appendix, in order to provide an overview of the differences between the different gear types.

Individuals caught were then selected for age analyses through one of the following selection procedures:

1. Selection of individuals per length class, proportional to the length distribution of the landing.
2. 25, 50, 50, 50, 50, 25, 25 and 25 individuals for analysis per every 2.5 cm length class, for length classes 12,6-15, 15,1-17,5… 27.6-30.0 cm.
3. 10 females per length group, in length groups 6(6.0-6.9), 7(7.0-6.9), … 11(11.0-11.9 cm) and 15 females per length group, in length groups 12(12.0-12.9), 13(13.0-13.9), … 20(20.0-20.9 cm) (Söderberg 2008).

In Holmön, method 1 was used in 1989-1991, method 2 in 1992-2002 and method 3 in 2003-2016 (Thoresson 1996). In Finbo, method 1 was used in 1977-1991, method 2 was used in 1991-2016 (Thoresson 1996). In Kvädöfjärden, method 2 was used in 1971-2001 and method 3 was used in 2002-2016 (Söderberg 2008). It is assumed that the data from these selection procedures is unbiased.

Back-calculated lengths at age were acquired from the fish selected from the test-fishing by relating the distance between yearly growth increments in hard structures (operculum bones in this case) to the length of the fish. This allows reconstruction of the growth trajectory of an individual fish during its life. The relationship between operculum bone and body length is defined through the equation:

$$L = 19.45 \cdot R^{0.861} \quad (1)$$

where L [mm] is the length at catch of an individual, R [mm] is the operculum radius and 19.45 as well as 0.861 are values attained from Agnedahl (1968). In order to acquire the actual annual lengths, the intermediate lengths from the operculum bones are corrected using equation:

$$L = L_s \cdot \left(\frac{l_i}{R}\right)^{0.861} \quad (2)$$

where L [mm] represent the back-calculated annual length, L_s [mm] is the body length at catch, l_i is the intermediate length (radius of the operculum bone from the centre to the corresponding annual growth ring) and R is the whole operculum bone radius [mm] (Thoresson 1996).

Back-calculated lengths at age were compiled for each area. Only growth between year increments was used for the analyses, resulting in a total of 112189 length estimates for 29197 female perch used in the

analyses. Male perch were excluded from the analyses as they differ from females in response to increased temperature (Lundgren 2015), and because male perch was not sampled during the entire study period. The results acquired from my analyses will consequently not be representative for the population as a whole but for female perch only. From Holmön, roughly 23500 observations of back-calculated length at age for 7526 female perch were compiled, ranging in birth year from 1982 to 2015. Approximately 48500 estimates of back-calculated length at age for 11063 female perch were compiled, ranging in birth year from 1969 to 2015, from Finbo. And lastly, from Kvädöfjärden, approximately 40000 estimates of back-calculated length at age for 10608 female perch were compiled, with birth years ranging from 1960 to 2015.

Statistical analyses of size and growth data

Length-at-age 1

Linear regression models were fitted to ln-transformed back-calculated body-length at age 1 estimates and temperature experienced during the birth year for each area in order to assess the response in body-length for one-year olds to increasing temperatures. The calculated body-length at age 1 estimates are given as mean $\pm$ two standard errors (SE $\times$ 2), if not otherwise stated.

Annual growth

Annual growth rates were calculated by setting the growth of the individual in relation to the size of the individual at the beginning of that growth year. An alternative would be to calculate the absolute growth, though it is less ideal when comparing growth rate of differently sized individuals (Lugert et al. 2016). Size-specific growth rate at age *a* at time *t* (henceforth SSG_t) was calculated for each individual using following equation:

$$SSG_{t,a} = \frac{\left(L_{t+1,a+1} - L_{t,a}\right)}{L_{t,a}} \cdot 100 \quad (3)$$

where a = age 1, 3, or 6, $L_{t,a}$ is the body length at time t and age a, L_{t+1} is the body length time $t+1$ and age $a+1$, multiplied by 100 to attain percentage increase in growth over time. Linear regression models were fitted to the annual $SSG_{t,a}$ estimates to test for temporal changes in growth rate. Further, regression models were fitted to the SSG_t for each year a with the average temperature of year t as explanatory variable to determine how well temperature explains the variation in size-specific growth rate for each age. The attained growth estimates are given as mean $\pm$ two standard errors (SE $\times$ 2), if not otherwise stated.

Life-span integrated growth rates

In eqn. 3, growth is measured between two subsequent years. However, growth in one year is not independent of the previous growth history of the individual. Therefore, it is important to also asses a measure of growth that integrates growth rates during the individual's life. To estimate growth rates across multiple ages within a cohort simultaneously, mean body-length at age for all ages were calculated within each cohort for each year. Annual absolute growth rates for the ages one to six of each cohort were then calculated as follows:

$$G_{t,a} = L_{t+1,a+1} - L_{t,a} \quad (4)$$

where a = age 1, 2… 6, $L_{t,a}$ is the mean body length at time t and age a, L_{t+1} is the mean body length time $t+1$ and age $a+1$. For each cohort, growth during the first year was equal to mean body length

at age one. Cohorts with birth year later than 2010 were excluded from the analyses as these did not contain all growth years. Within each cohort, all mean body lengths at age along with corresponding growth rates for each growth year (calculated from eqn. 4), were then used to fit the following model, which integrate the growth rates experienced during the individual's life:

$$G(L_{t,a})_c = \alpha \cdot e^{(\beta \cdot L_{t,a})} \quad (5)$$

where growth of $G(L_{t,a})_c$ is estimated for each cohort c as a function of length at age a and time t, and accounts also for the size-dependence of growth. The parameters α and β were estimated by fitting a linear model to eqn. 5 on a natural log-scale:

$$ln(G(L_{t,a})_c) = ln(\alpha) + \beta \cdot L_{t,a} + \varepsilon_t \quad (6)$$

where $ln(G(L_{t,a})_c)$ is the natural log of size-dependent growth rate, $L_{t,a}$ is the mean length at time t and age a in $G(L_{t,a})_c$, $ln(\alpha)$ is the intercept (that is, the size-independent growth rate) and β is the slope, which captures the linear decline of the natural logarithm of growth with length. The model of each cohort attained from eqn. 6 where used to calculate mean size-dependent growth for three different size classes, small, medium and large for each area. Size classes used for growth analyses in each area were following, 50, 145 and 240 mm. The calculated growth rates for each size class were then divided with the length of the corresponding length class to express it per unit length (size-specific). The estimated growth rates for the specific sizes were regressed against time (birth year) and against different sets of mean temperatures. The calculated growth estimates are given as mean $\pm$ two standard errors (SE $\times$ 2).

The following temperature variables were used when analysing changes in size-specific growth for these three size classes:

1. Birth year temperature (50 mm class)
2. Mean temperature experienced at age 3 and 4 (145 mm class)
3. Mean temperature experienced at age 5 and 6 (240 mm class)

The software R, version 3.2.1 (R Core Team, 2015) was used for data collation and statistical analysis. All models were checked for assumptions on normal distribution of residuals and homoscedasticity (equal variance) using graphical methods (Figure A8-A46 in Appendix).

Results

Temperature

Mean SSTs in August increased significantly ($p<0.001$) between 1970 and 2016 in all areas. The temperature increase during this period was 0.049 [°C Year^{-1}] in Finbo, 0.045 [°C Year^{-1}] in Holmön and 0.037 [°C Year^{-1}] in Kvädöfjärden (Figure 2).

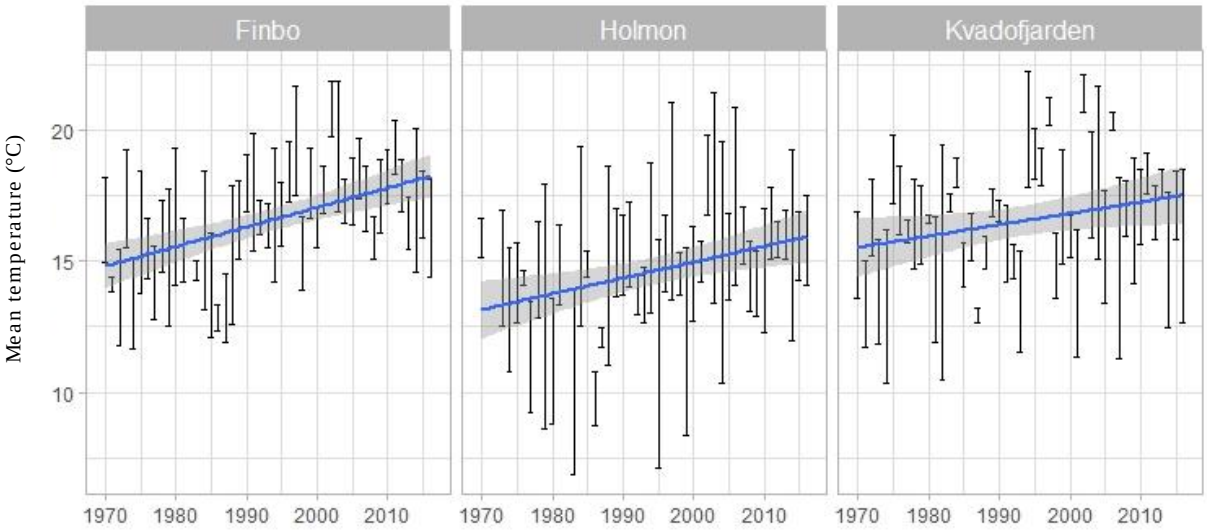

Figure 2. Annual August sea surface temperature (SST) in Finbo, Holmön and Kvädöfjärden between 1970 and 2016. Blue lines represent the fitted model predictions along with standard deviation bars and a 95% confidence interval (grey) of each prediction.

Length at age 1

A positive, significant ($p<0.001$) relationship between ln-transformed body length at age one and mean August SSTs was found in each area. Length at age one is assumed to be representative of growth in the first year. The increase in length at age one with temperature was greatest in following order: Holmön, with an increase of 0.032 ± 0.002 (SE × 2) [ln(mm) $°C^{-1}$], Finbo, with an increase of 0.029 ± 0.0014 and Kvädöfjärden, with an increase of 0.02 ± 0.0013. Based on the regression model equations, an increase from 13°C to 18°C would increase body-length as following: from 62.8 to 73.7 mm in Holmön, 59.4 to 68.6 mm in Finbo and 64.3 to 71.1 mm in Kvädöfjärden (Figure 3). The low adjusted r^2 values of the models indicate that temperature does not explain the variation in body-length well. Residual plots for each model are found in Figures A8, A9 and A10 in the Appendix.

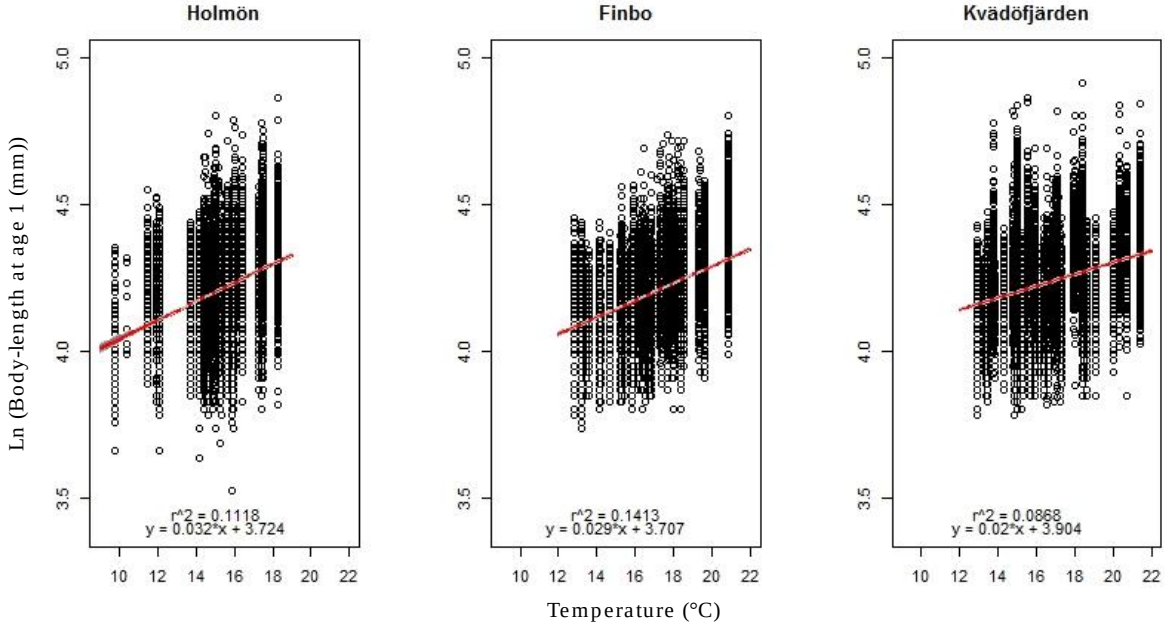

Figure 3. Relationship between ln-transformed body-length at age one and birth year temperature. The red lines represent the fitted model predictions along with a 95% confidence interval (grey) of each prediction. The confidence intervals are narrow and hardly visible in the figures.

Annual growth

Size-specific annual growth rates at age increased significantly with temperature for all three ages and in all locations, except for six-year old perch in Holmön. The strongest effect of temperature on size-specific growth was found for age one in all areas (Holmön, 3.66 $\pm$ 0.34 (SE × 2) [mm mm^{-1} Year^{-1} °C^{-1}], Kvädöfjärden 2.98 $\pm$ 0.21, and Finbo 2.56 $\pm$ 0.2). The effect decreased in magnitude but remained positive for all other ages (Figure 4). The adjusted r^2 values were low in all models. See Table A1 for model summaries and Figures A11 to A28 for residual plots of each model in the Appendix.

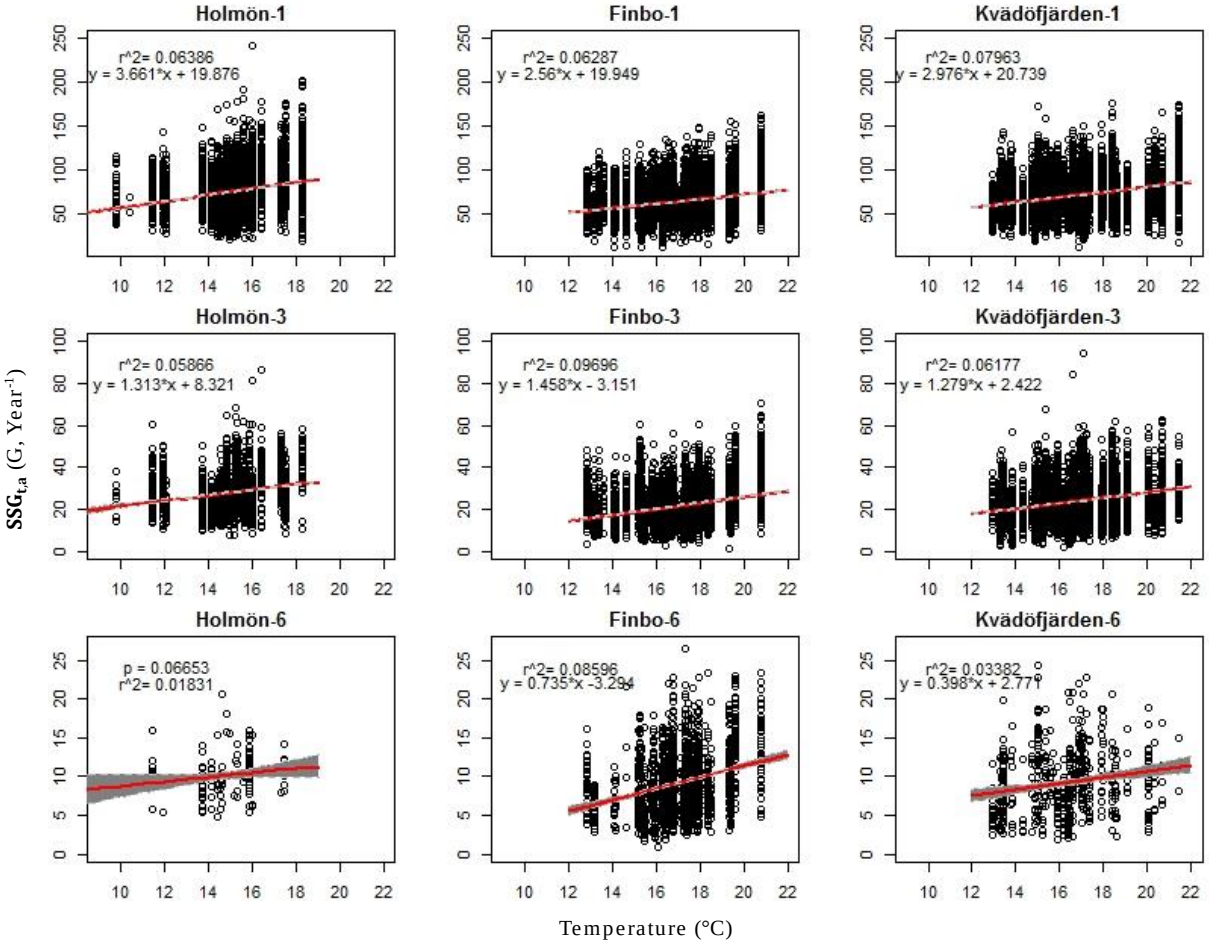

Figure 4. Size specific growth for $SSG_{t,a=1,3,6}$ (percentage increase in length) (eqn. 3), regressed against temperature of year t. Top row is growth year one, mid row is growth year three and bottom row is growth year six. The red line of each subplot is the model prediction along with a 95% confidence interval (grey) of the prediction.

Life-span integrated growth rates

The life span integrated growth rate $G(L_{t,a})_c$ of size classes 50 mm, 145 mm and 240 mm perch all increased significantly over time, in all locations, except for the 240 mm size class in Holmön (Figure 5). Size class 50 mm in all areas demonstrated a higher increase in $G(L_{t,a})_c$ over time than the 145 and 240 mm classes. The greatest increase in growth rate was in the 50 mm size class and was as following, Holmön (0.695 $\pm$ 0.5 (SE × 2) [mm Year^{-1} Year^{-1}]), Kvädöfjärden (0.68 $\pm$ 0.55) and Finbo (0.34 $\pm$ 0.325) (see Table A2 in the Appendix for model summaries). Moreover, $G(L_{t,a})_c$ in size classes 145 mm and 240 mm were generally higher in Holmön than in Finbo and Kvädöfjärden (Figure 5). One outlier positioned beyond Cooks distance of 0.5 (Cook 1977) were removed from the analysis of Holmön class 50 mm (data representing 2002). For residual plots of each model, see Figures A29 to A37 in the Appendix.

Further, significant relationships were found between $G(L_{t,a})_c$ and temperature for all size classes in Finbo, as well as for the 145 mm size class in all areas (Figure 6). In Finbo, the response in $G(L_{t,a})_c$ towards increasing temperatures for each size class was strongest in the following order: 50 mm size class (0.05 ± 0.043 (SE × 2) [mm Year^{-1} mm^{-1} °C^{-1}]), 145 mm size class (0.015 ± 0.005) and 240 mm size class (0.0096 ± 0.0036). For the 145 mm size class, the strongest response to increasing temperature per area was as following: Finbo (0.015 ± 0.005 [mm Year^{-1} mm^{-1} °C^{-1}]), Kvädöfjärden (0.01 ± 0.009) and Holmön (0.0065 ± 0.006) (see Table A3 in the Appendix for model summaries). One outlier positioned beyond Cooks distance of 1.0 (Cook 1977) was removed from the analysis of Holmön 50 mm (the point representing 2002). For residual plots of each model, see Figures A38 to A46 in the Appendix.

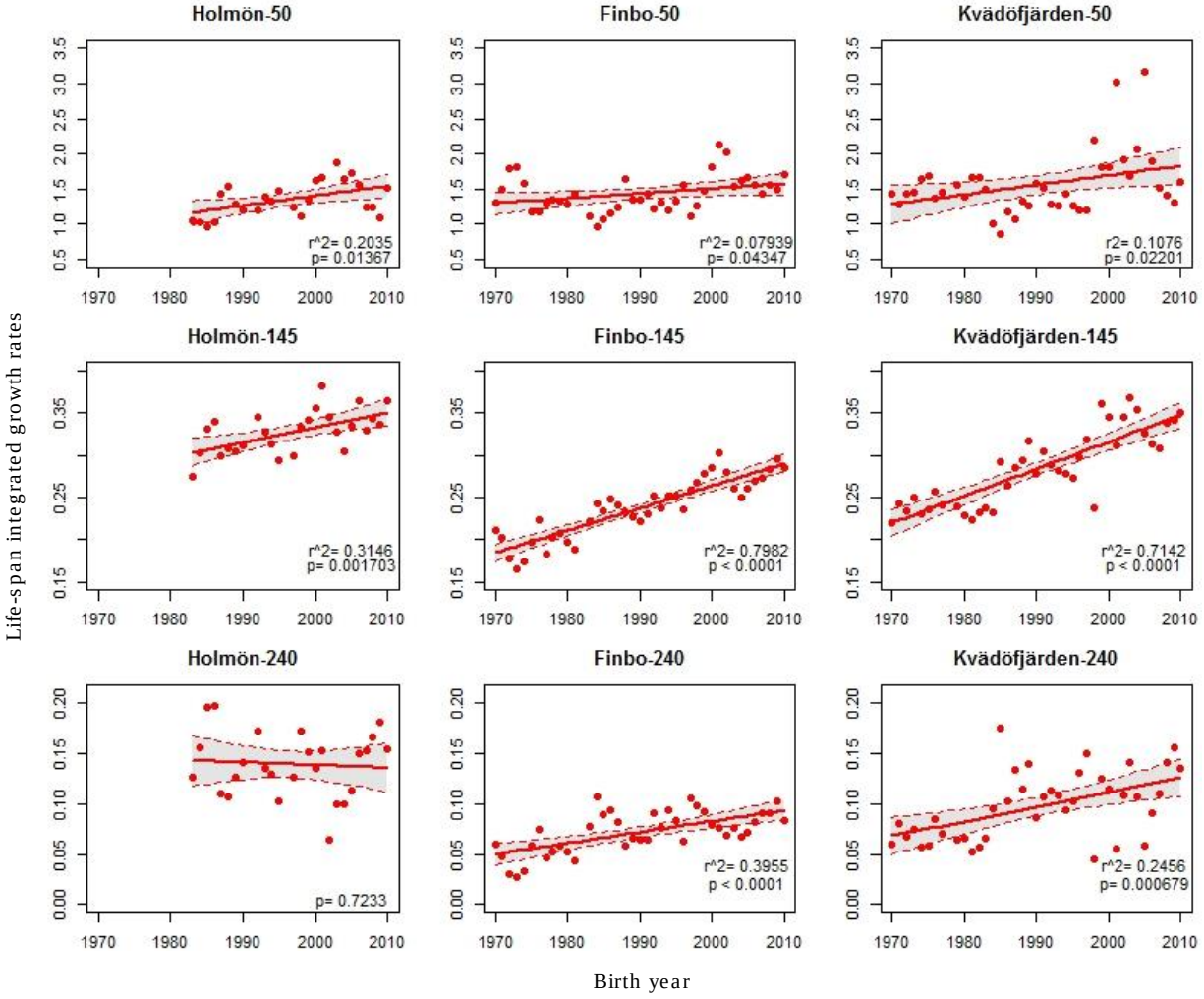

Figure 5. Predicted life span integrated growth rates [mm Year^{-1} mm^{-1}] (eqn. 5) for three size classes regressed against time (birth year). The red line of each subplot is the model prediction along with a 95% confidence interval (grey). Top row is the 50 mm class, mid row is the 145 mm class and bottom row is the 240 mm size-class.

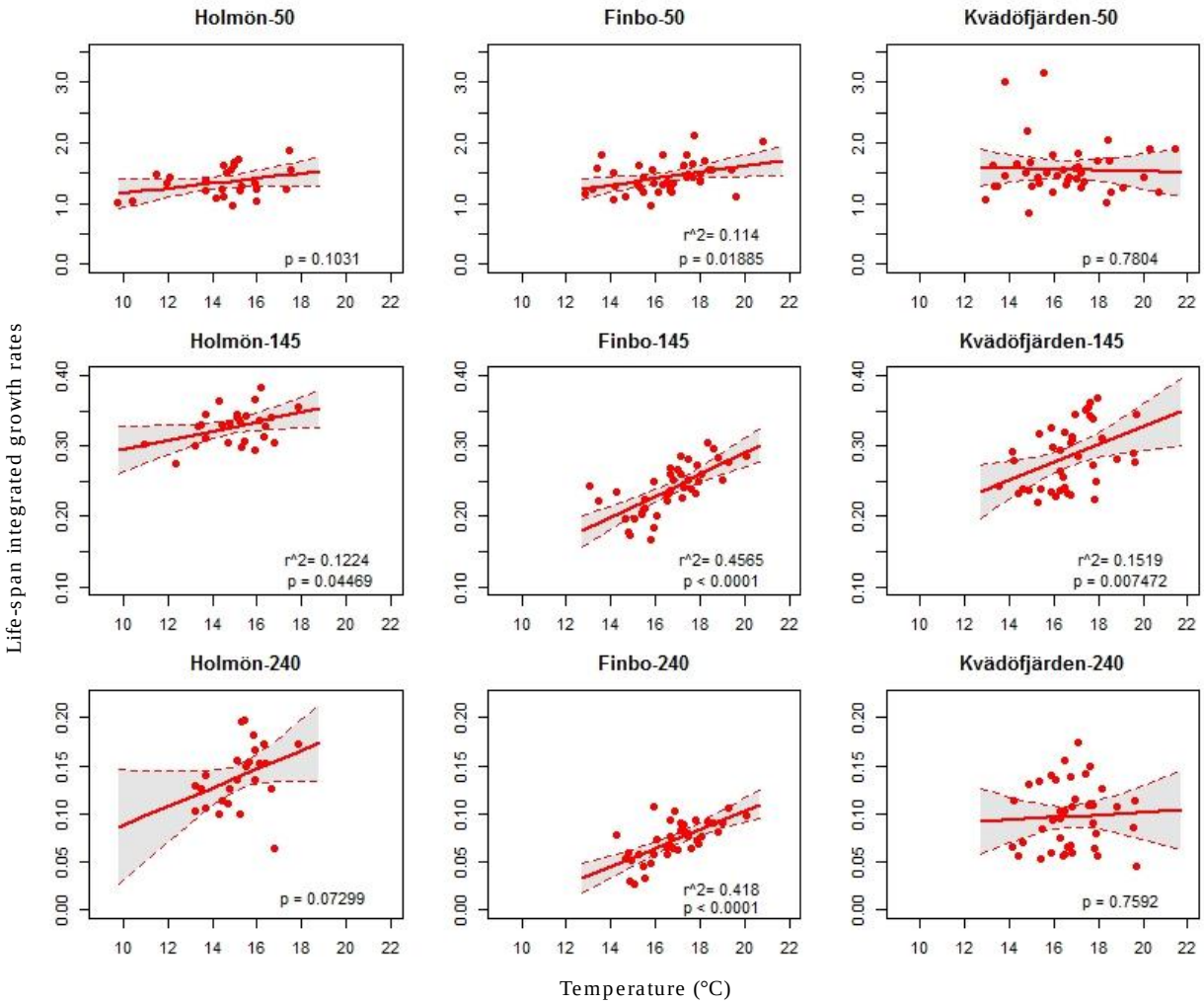

Figure 6. Predicted life span integrated growth rates [mm Year^{-1} mm^{-1}] (eqn. 5) for three size classes regressed against different temperature variables. The red line of each subplot is the model prediction along with a 95% confidence interval (grey). Top row is the 50 mm class, mid row is the 145 mm class and bottom row is the 240 mm size-class.

Discussion

This study attempts to answer whether body growth and length at age for perch have been affected by increasing temperatures and how the response differs between populations in areas of different latitudes. My analyses of four decades of back-calculated length at age data from three areas in the Baltic Sea demonstrated a positive relationship to temperature of both body length at age one and size specific growth at age ($SSG_{t,a}$). The increase in growth of younger age classes with temperature is consistent with findings in other species in studies of Baudron et al. (2014), Rindorf et al. (2008) and Thresher et al. (2007). Also size specific life-span integrated growth in different size classes, the 145 mm class of Holmön and Kvädöfjärden, along with all size classes in Finbo demonstrated positive relationships between growth and increased temperature. In Finbo, the growth response decreased with body size, which is consistent with the findings of Lundgren (2015) from a long-term heating study, that smaller perch have a stronger response to increased temperature than large.

My results further suggest that the body-length at age one, as well as growth response for young perch in growth year one and two, differ over a latitudinal gradient, with the strongest response to increasing temperatures in the north. In the body-length at age one analyses, the confidence intervals (CI) of the responses in Holmön and Finbo overlapped, while the CI of Kvädöfjärden overlapped with none,

suggesting that the response in Kvädöfjärden may be different from Holmön and Finbo. In the analyses of size specific growth at age ($SSG_{t,a}$) the CI did not overlap for any area in growth year one (although they were close), which suggest that the growth response may differ between all areas. The pattern of stronger response in the north may be explained by a broader thermal safety margin (TSM), and thermal tolerance (roughly equal T_{opt} for growth between the populations, but lower minimum critical temperature in the north) which would possibly allow the northern populations to grow relatively faster at lower temperatures, than the central and southern populations. This is a pattern found in terrestrial insects by Deutsch et al. (2008), with increasingly broader thermal tolerance from low to high latitudes and that high latitude insects may initially benefit from the warming. However, though both ectothermic, it cannot be assumed that fish generally follow the same pattern as terrestrial insects do, although it has been shown by Conover & Schultz (1997), that northern strains of fish species grown in aquacultures have a greater production potential than the southern strains do, relating to the differences in growth potential. Further, since all my areas are located at "high latitude" within the boreal forest biome, it may be questioned whether the pattern described by Deutsch et al. (2008) is perceivable on a scale of only two-three degrees differences in latitude. While a difference in the strength of the growth response from north to south was found for perch in growth year one and two, no such pattern was found for perch in older growth years. It was neither found for size-specific growth rate of medium-size perch (145 mm), where the growth response was strongest in following order; central, south and north. The explanation why the growth response of older age classes and perhaps the 145 mm size class do not follow the same pattern as young perch, may be related to local variations in factors such as oxygen and food, which also determines growth. A limitation of these factors would affect the growth of larger (usually older) individuals more, as growth in large perch is less resilient than growth in small perch, i.e. due to differences in resource allocations. Most of the energy up until maturation is put into growth of somatic cells (Enberg et al. 2012). Further, limitations in oxygen or food is not necessarily connected to the latitude of area, thus one would not anticipate a difference in growth response over a latitudinal gradient.

Temperature was the only variable used to explain the variation in growth in my analyses, which is a limitation, as growth is also highly dependent on food and oxygen supplies. The low adjusted r^2 values attained from my growth models further corroborates the limitation of temperature as a single explanatory variable. Considering food supply, the Baltic Sea is nutrient rich due to decades anthropogenic nutrient loading (Elmgren 2001), however if the nutrient loading has translated into an abundance of food for perch from age one to six, remains obscured, as the access to food is also influenced by e.g. inter- and intra-specific competition, which may in turn be affected by e.g. mortality, as increased mortality by e.g. predation or cannibalism reduces competition. Further, considering oxygen supply, the only part of the Baltic Sea that regularly suffers from oxygen deprived bottoms is the Baltic Proper (Carstensen et al. 2014), and not so much the Gulf of Bothnia. Oxygen deprived bottoms affect the growth of perch as it may restrict perch from feeding on zoobenthos, thus leaving perch with the only option to feed on zooplankton. Another unaccounted aspect is the possibility that perch may have undergone adaptions during the studied period, e.g. earlier maturation which would mainly affect the growth rate of subadults, as they grow at a higher rate up until maturation than after.

The main challenge in this study was to achieve a representative dataset for temperature in each area. First, is assumed that the ICES temperature is relevant to the areas, which is supported in Figures A1 and A2 for Holmön and Finbo. In Kvädöfjärden however, the ICES temperature relevance cannot be substantiated as there are large gaps in the time-line of the in-situ measured observations (Figure A3). Secondly, it is in this study assumed that mean August temperatures can be used as a proxy for the entire growth season, which is problematic as the growth season extends over several months from spring to early fall. Thirdly, sample size per year varied from year to year, which on occasion resulted in high

number of temperature observations in some years and few in others. As such, for a couple of years, only a handful of temperature observations in August represented the mean temperature for the entire growth season, which may not be a very representative measure of the temperature of that year. In order to address the second and third problem, August temperature means were compared to the mean temperature of months May to September in each area, with positive, significant correlations found in all areas. More specifically, using Pearson's product moment correlation coefficient, following values were obtained, r = 0.78 in Holmön, r = 0.73 in Finbo and r = 0.54 in Kvädöfjärden (Figure A4 in the Appendix), indicating that the August temperatures provide a relevant measure of the long-term variation in temperature relevant for perch growth, and that it can be assumed to be an acceptable proxy in analysing general patterns across the four decades studied. Further, the temperature variables used for the analyses on size classes may have been suboptimal. In order to get a direct comparison between the growth responses to increasing temperature between the areas, temperatures experienced during the same years of age were used. Thus, for the size class 145 mm, temperature means were calculated from temperatures experienced between age three and four. This is problematic as perch differ in size at age between the areas. At the size 145 mm in Holmön, the majority of perch is between age two and three, in Finbo age three and four, and in Kvädöfjärden age three. Further, the growth of the 240 mm size class was regressed against temperature means from temperatures experienced between age five and six. At 240 mm the majority of perch in Holmön is between age four and five, in Finbo age five and six, and in Kvädöfjärden age five. Though still relevant, the temperature regressed against growth at sizes 145 and 240 mm will mismatch relatively more for perch in Holmön and Kvädöfjärden than in Finbo. In regard to this, it may be suggested that the result attained in the 145 and 240 mm size class of Holmön and Kvädöfjärden should be interpreted with more caution than the result attained from Finbo.

Different fishing gears were used, and the procedures of selecting individuals for analysis changed over time. Though assumed in this study that a change in fishing gear or selection procedure does not bias the result, it may have had an effect. When comparing data on fish caught before and after gear shifts, the most noteworthy pattern was the generally low abundance of one-year old perch in the period before the shifts, compared to the abundance after the shift, in all three areas (Figures A5, A6 and A7 in the Appendix). This is expected, as the gear used in the later period includes nets with smaller mesh size than the previously used gear. Further, the procedure of selecting individuals changed from method two to method three (see method section) at the time of fishing gear shift in Holmön, and in so, changed the minimum length class of selected individuals from 12.6 - 15 cm, to a minimum length class of 6.0 – 6.9 cm which may explain the sudden appearance of one-year old perch after the shift, at least in Holmön. The shift in fishing gear could have biased the results of the body-length at age one analyses, as the nets with larger mesh size would catch more fast-growing, large one-year-olds than nets with smaller mesh size. This would primarily be manifested as higher growth rates in one-year-olds before the gear shift. However, as the analyses of body-length at age one were performed on mainly back-calculated length estimates and not on length-at-age when caught, it may be suggested that the effect of gear shift is minimal.

Moreover, though my results suggest that body length at age one and growth response for young perch in their second growth year (between age one and two) differ over a latitudinal gradient, with the strongest response to increasing temperatures in the north, it has not been tested in a statistical model whether the response from each area are significantly different from each other, which limits the ability to conclude this pattern.

Conclusion

Both body length at age one and size specific annual growth rates at age ($SSG_{t,a}$) have increased with increasing temperatures in all locations. Further, lifespan integrated size-specific growth rate for all size classes of Finbo and for the 145 mm class of Holmön and Kvädöfjärden demonstrated positive relationship to increasing temperatures. Although temperature did not explain much of the variation in growth and size, these results are indicative of that warming has increased perch growth in the Baltic Sea. Moreover, my results suggest that the response in body length at age one, and the growth responses in growth year one and two to increased temperatures were all comparatively stronger in the north, than in the central and the south of the Baltic Sea, although no statistical test of latitudinal differences in the response were carried out in this study. It may, however, suggest that the growth response in young perch changes with latitude, with the strongest response to increased temperatures in the north, which indicates an important avenue for further research.

This information may be useful when making predictions on how continued increases in temperature may affect the growth and body length of perch. As growth shapes body size, which in turn affects the ecological function of perch, the change in growth to increased temperature may be used for making predictions on how further warming may affect the growth and size of perch and ultimately its ecological function in ecosystems. Further, though not statistically tested in this study, the indications of differences of responses between areas found may also help to generate future understanding of how the response in growth may change over latitude.

In future studies, it would be useful to include perch of even larger sizes, as it is unclear how they respond in growth and size to increasing temperature. It would also be of interest to include perch from lower latitudes, where one might expect the increased warming to have resulted in a classic TSR response. It would further be useful to include additional variables in the analyses on growth response, i.e. oxygen and food supply, as these greatly affect growth as well.

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Appendix

Table A1. Model summaries from linear regressions of $SSG_{t, a= 1,2,3,4,5,6}$ estimates and mean temperature experienced during the year of growth.

Area	$SSG_{t,a=1,2,3,4,5,6}$	Equations of growth and temperature	p-value
Holmön	1	y = 3.661*x + 19.876	p<0.0001
	2	y = 1.894*x + 15.926	p<0.0001
	3	y = 1.313*x + 8.321	p<0.0001
	4	y = 1.645*x - 5.844	p<0.0001
	5	y = 0.959*x - 0.765	p<0.0001
	6	y = 0.284*x + 5.954	p<0.0665
Finbo	1	y = 2.56*x + 19.949	p<0.0001
	2	y = 0.91*x + 19.411	p<0.0001
	3	y = 1.458*x - 3.151	p<0.0001
	4	y = 0.586*x + 4.713	p<0.0001
	5	y = 1.049*x - 6.764	p<0.0001
	6	y = 0.735*x - 3.294	p<0.0001
Kvädöfjärden	1	y = 2.976*x + 20.739	p<0.0001
	2	y = 1.546*x + 13.71	p<0.0001
	3	y = 1.279*x + 2.422	p<0.0001
	4	y = 0.572*x + 7.00	p<0.0001
	5	y = 0.845*x - 1.838	p<0.0001
	6	y = 0.398*x + 2.771	p<0.0001

Table A2. Model summaries from linear regressions of life span integrated growth and birth year for size classes 50, 145 and 240 mm. Asterisks in the "Size-class" column expresses statistical significance.

Area	Size class [mm]	Equations for growth over time (birth year)	p-value	r^2
Holmön	50*	y = 0.01391*x - 26.418	p<0.0136	0.2035
	145*	y = 0.001736*x - 3.139	p<0.0017	0.3146
	240	y = -0.000275*x + 0.689	p<0.7233	-
Finbo	50*	y = 0.006839*x - 12.177	p<0.0434	0.0793
	145*	y = 0.002651*x - 5.038	p<0.0001	0.7982
	240*	y = 0.001093*x - 2.103	p<0.0001	0.3955
Kvädöfjärden	50*	y = 0.013613*x - 25.533	p<0.022	0.1076
	145*	y = 0.003196*x - 6.077	p<0.0001	0.7142
	240*	y = 0.001445*x - 2.779	p<0.0006	0.2456

Table A3. Model summaries from linear regressions of life span integrated growth regressed against different sets of temperature for size class 50, 145 and 240 mm. Asterisks in the "Size-class" column expresses statistical significance.

Area	Size class [mm]	Equations for growth, birth year temperature	p-value	r^2
Holmön	50	y = 0.040918*x + 0.764	p<0.1031	-
	145*	y = 0.006524*x + 0.23	p<0.0446	0.1224
	240	y = 0.009696*x - 0.009	p<0.0729	-
Finbo	50*	y = 0.052163*x + 0.578	p<0.0188	0.114
	145*	y = 0.015231*x - 0.014	p<0.0001	0.4565
	240*	y = 0.009599*x - 0.089	p<0.0001	0.418

Kvädöfjärden	50	y = -0.009656*x + 1.72	p<0.7804	-
	145*	y = 0.012641*x + 0.074	p<0.0074	0.1519
	240	y = 0.001208*x + 0.077	p<0.7592	-

Table A4. ICES temperature, test of bias in time and water depth sampled over the years. Error-terms are removed as they occur in each model.

Area	Variables	p-value
Holmön	mean week = α + β*year	p<0.54
Holmön	mean week = α + β*mean temp	p<0.006
Holmön	mean depth = α + β*year	p<0.16
Holmön	mean depth = α + β*mean temp	p<0.71
Finbo	mean week = α + β*year	p<0.26
Finbo	mean week = α + β*mean temp	p<0.49
Finbo	mean depth = α + β*year	p<0.9
Finbo	mean depth= α + β*mean temp	p<0.045
Kvädöfjärden	mean week = α + β*year	p<0.09
Kvädöfjärden	mean week = α + β*mean temp	p<0.47
Kvädöfjärden	mean depth = α + β*year	p<0.24
Kvädöfjärden	mean depth = α + β*mean temp	p<0.03

Table A5. Fishing gear specifications.

Gear type	Length (m)	Depth (m)	Mesh-size (mm)
Survey gillnet	35	3	17, 22, 25, 33 and 50
Nordic survey gillnet	45	1.8	30, 15, 38, 10, 48, 12, 24, 60 and 19
Gillnet (biologiska länkar)	27	1.8	21.5 - 60
Gillnet (nätlänkar, 2-5m depth)	27	1.8	17, 21, 25 and 30
Gillnet (nätlänkar, 14-20m depth)	27	1.8	21, 30, 38, 50 and 60

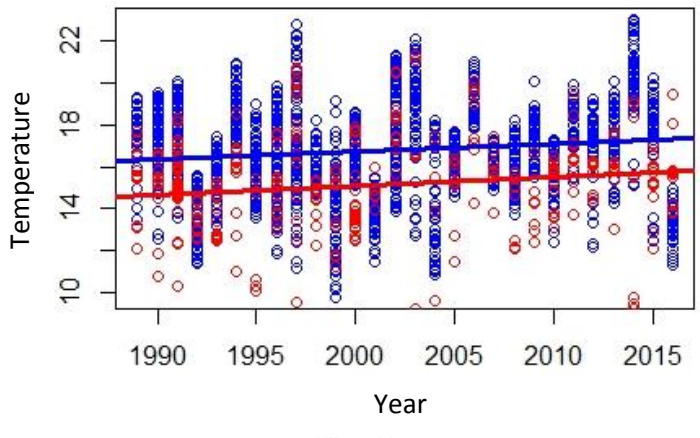

Figure A1. Two regression models fitted against temperature observations and time in Holmön. Predicted lines are based on temperature observations acquired from ICES datasets and SLU dataset. Red is the ICES temperature and blue is the SLU temperature.

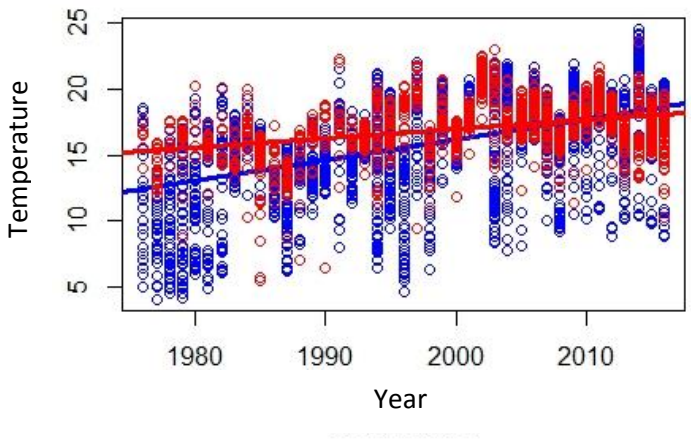

Figure A2. Two regression models fitted against temperature observations and time in Finbo. Predicted lines are based on temperature observations acquired from ICES datasets and SLU dataset. Red is ICES data, blue is SLU data.

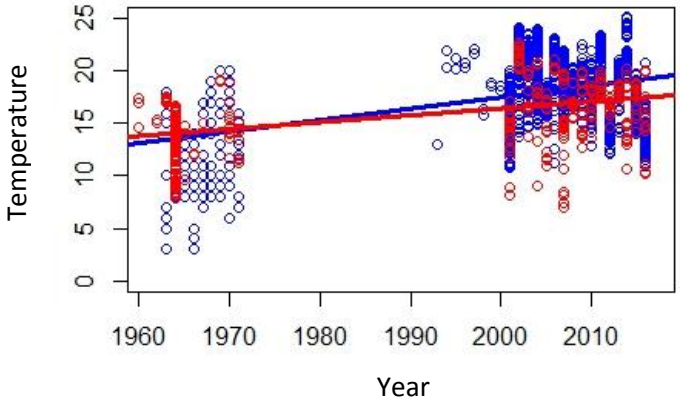

Figure A3. Two regression models fitted against temperature observations and time for two time-periods in Kvädöfjärden. Predicted lines are based on temperature observations acquired from ICES datasets and SLU dataset. Red is ICES data, blue is SLU data.

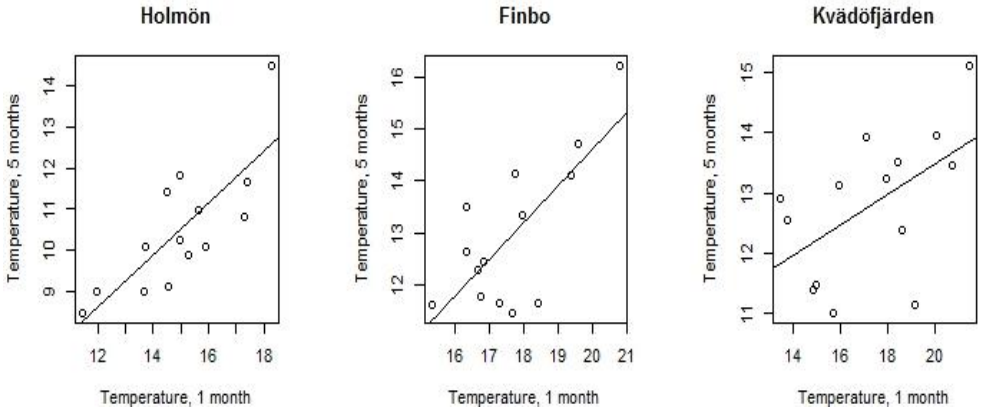

Figure A4. Correlated August temperature with temperature mean for the growth season (May to September) in the period 1991 to 2004. r (12) = 0.78, p< 0.001, two-tailed in Holmön, r (12) = 0.73, p= 0.003, two-tailed in Finbo and r (12) = 0.54, p=0.048, two-tailed in Kvädöfjärden.

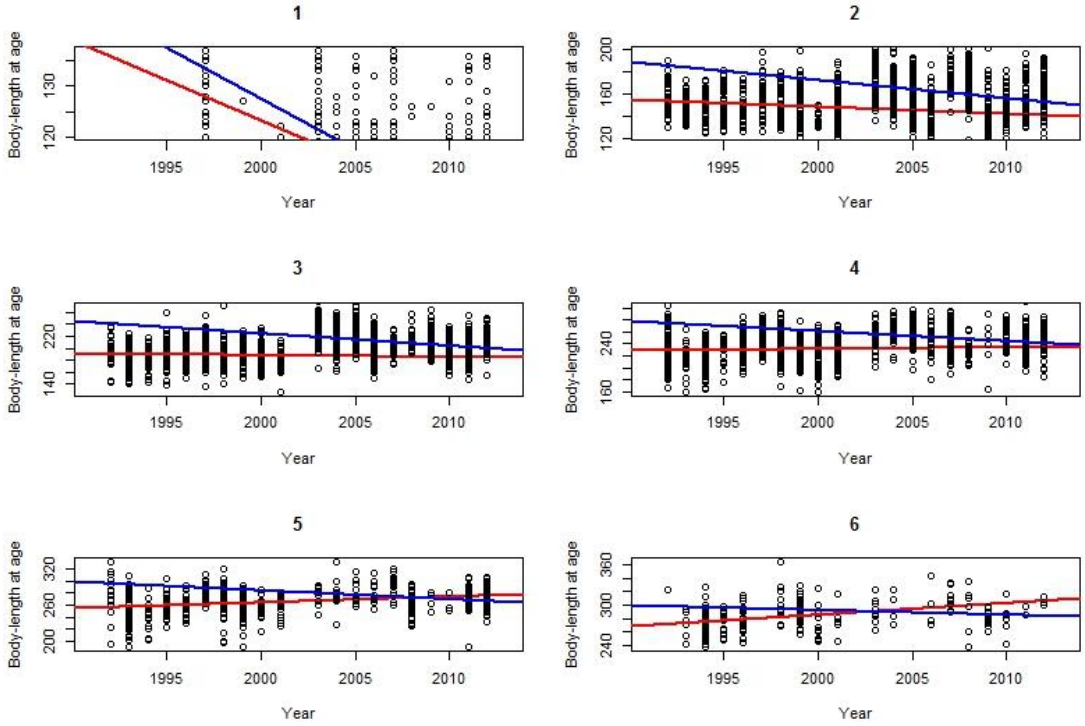

Figure A5. Body-length development in Holmön before and after fishing gear shift for ages 1 to 6. Red line represents the predicted body length development at age in the period 1992 to 2002 and blue the period 2002 to 2012.

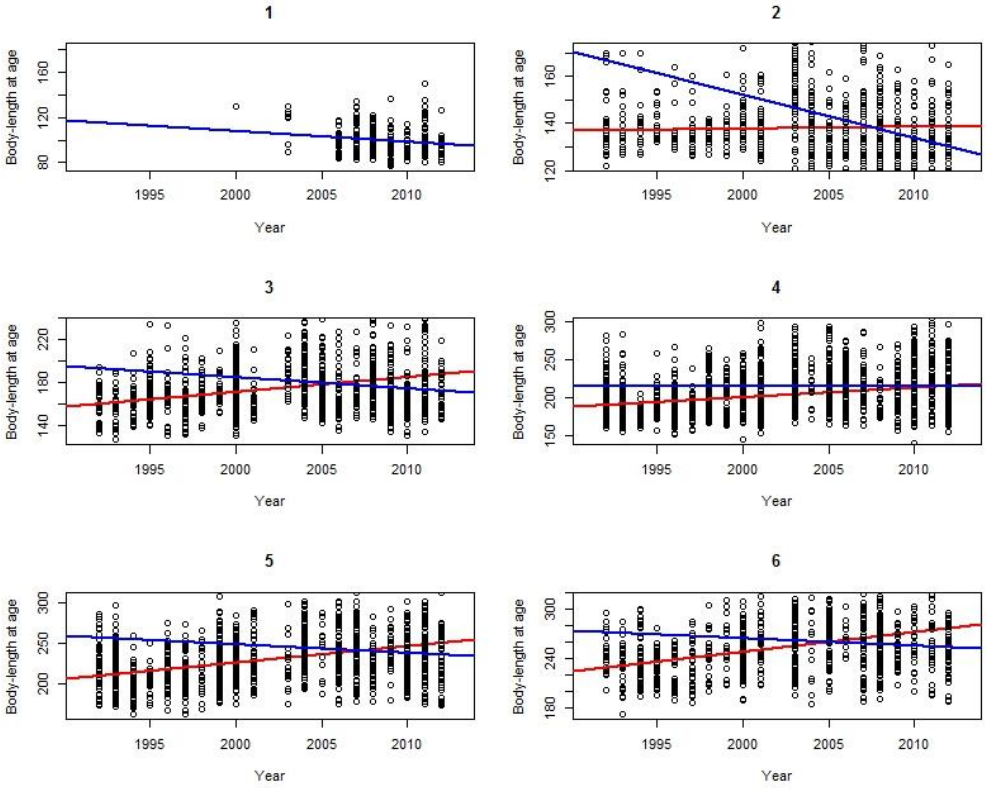

Figure A6. Predicted body-length development in Finbo before and after fishing gear shift for ages 1 to 6. Red line represents the body length development at age in the period 1992 to 2002 and blue the period of 2002 to 2012.

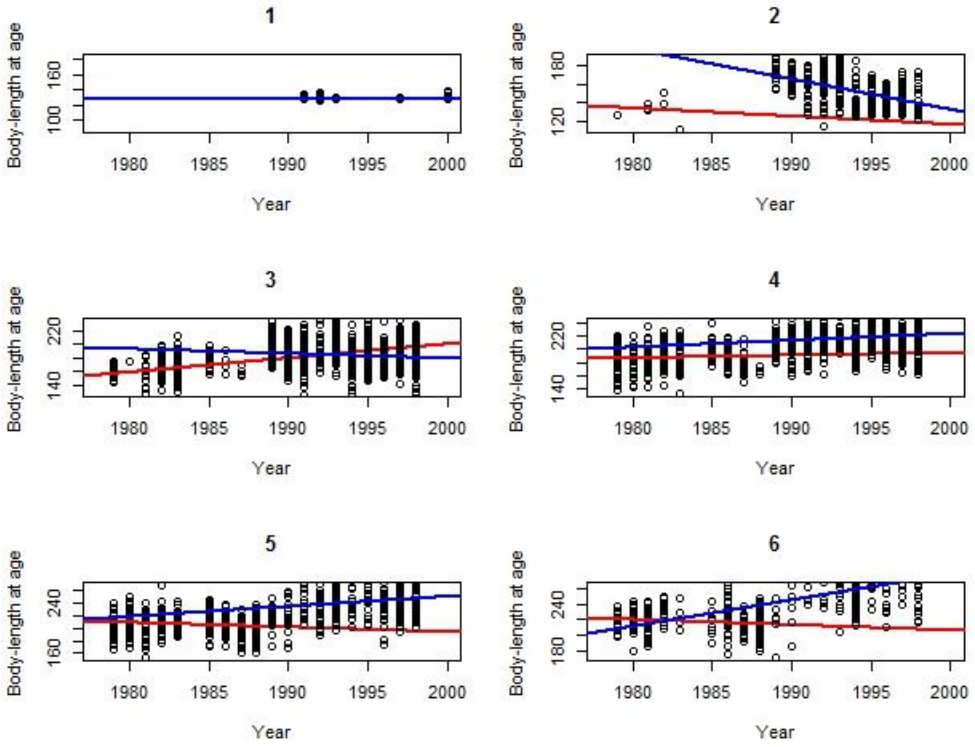

Figure A7. Predicted body-length development in Kvädöfjärden before and after 1989 for ages 1 to 6. Red line represents the body length development at age in the period 1979 to 1989 and blue line represent 1989 to 1999.

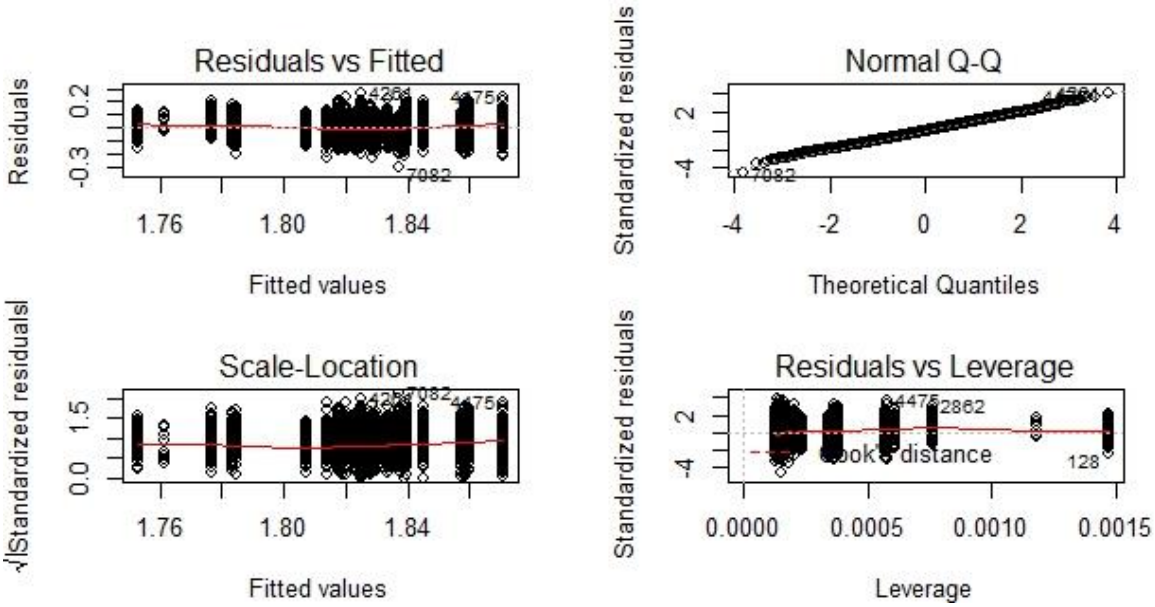

Figure A8. Plot of residuals from the analysis of Holmön. Body length of 1-year old perch.

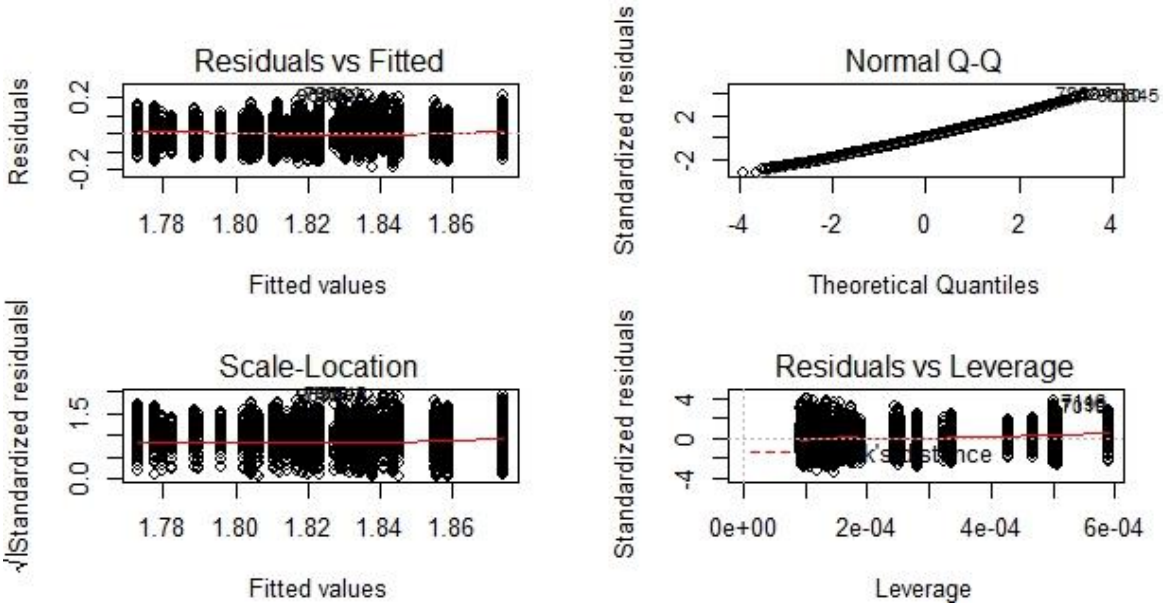

Figure A9. Plot of residuals from the analysis of Finbo. Body length of 1-year old perch.

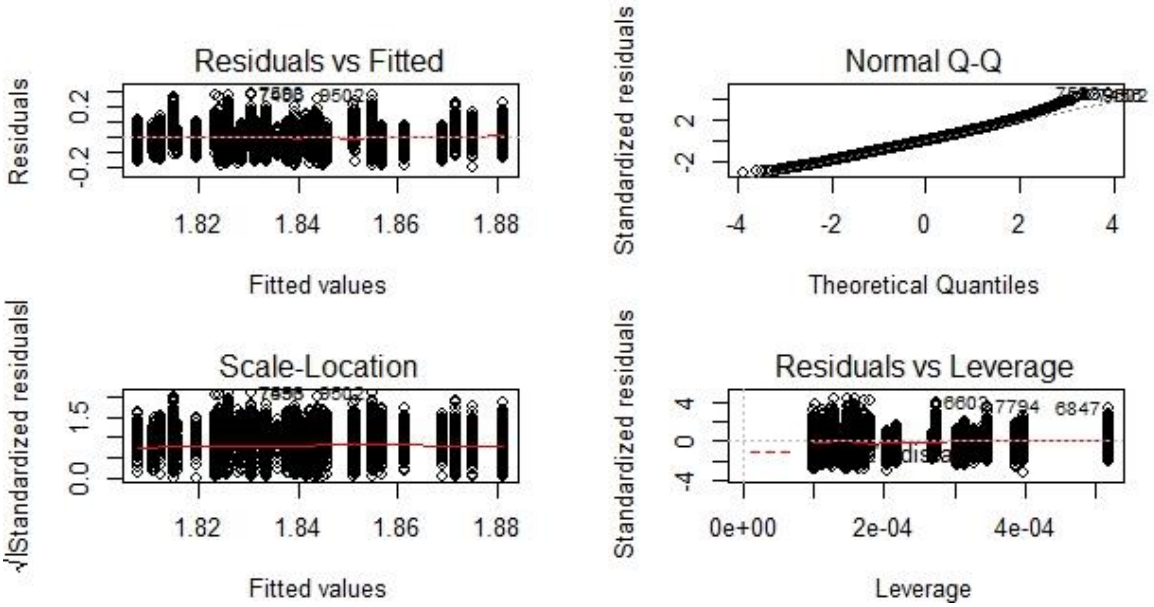

Figure A10. Plot of residuals from the analysis of Kvädöfjärden. Body length of 1-year old perch.

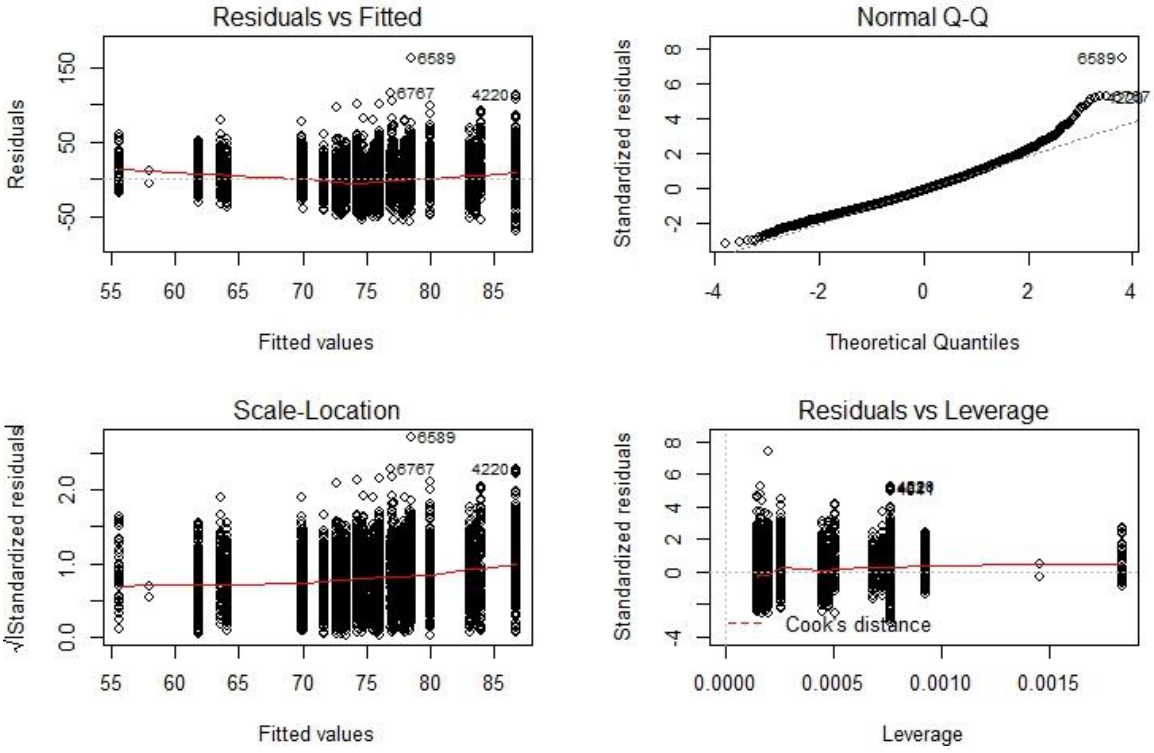

Figure A11. Plot of residuals from the analysis of Holmön. Age 1.

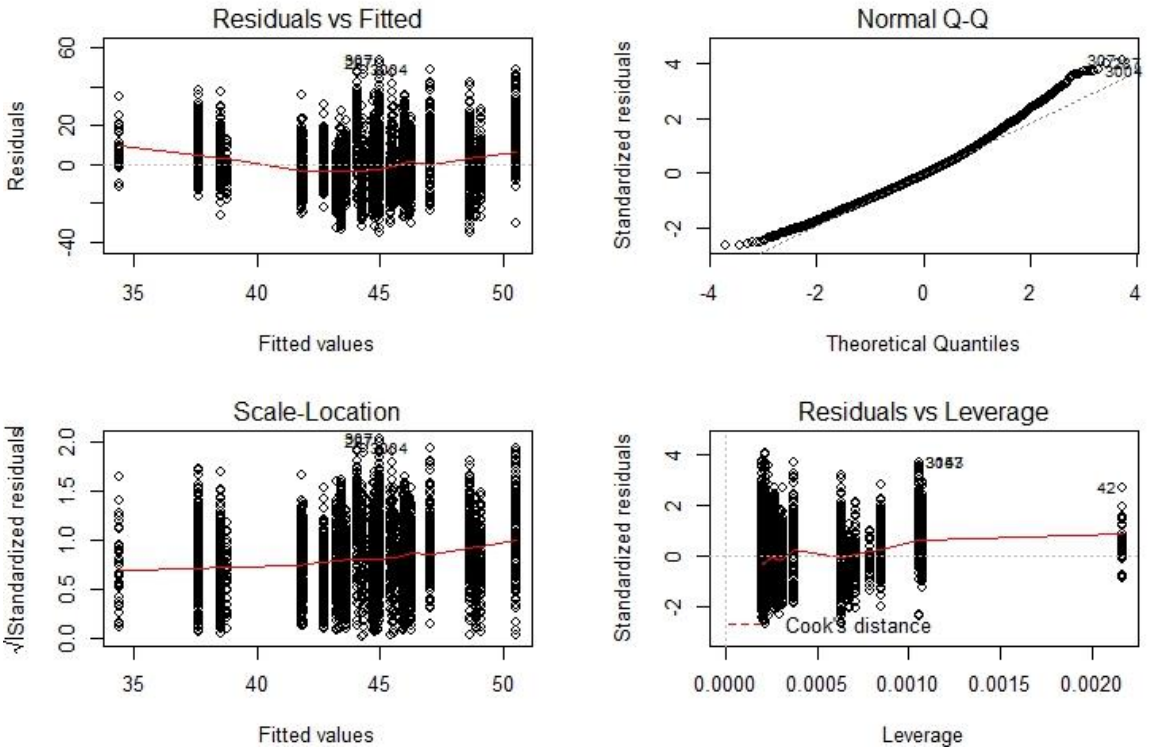

Figure A12. Plot of residuals from the analysis of Holmön. Age 2.

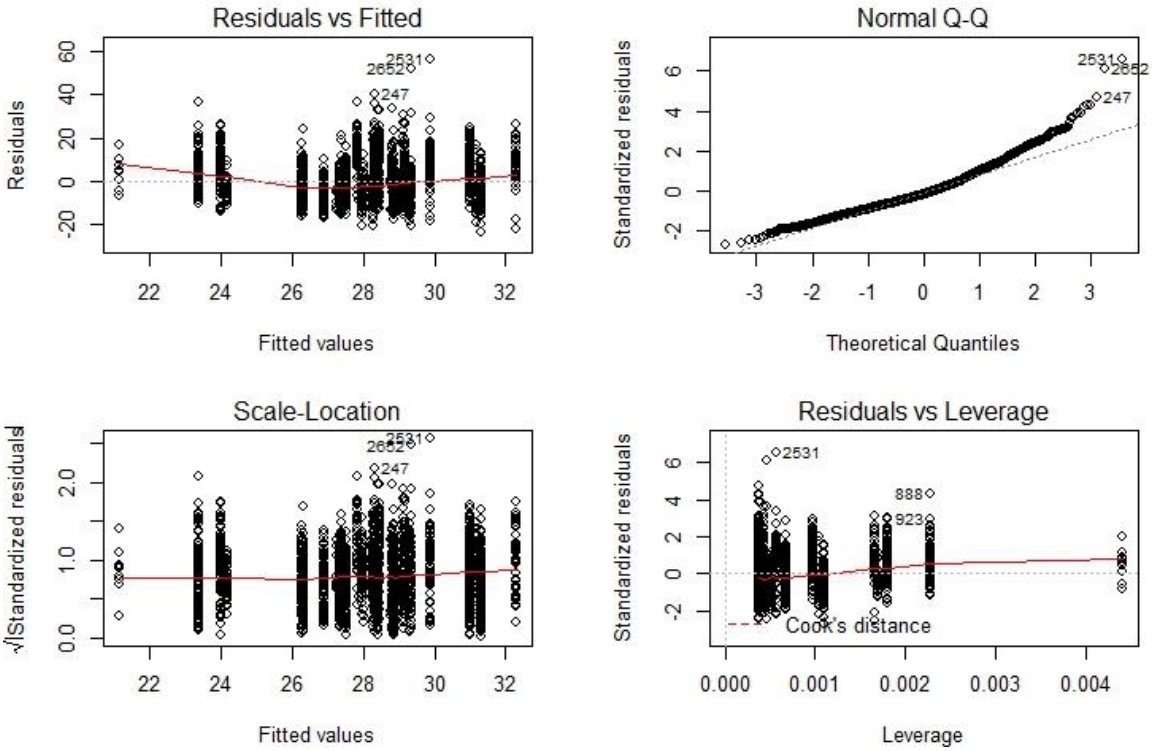

Figure A13. Plot of residuals from the analysis of Holmön. Age 3.

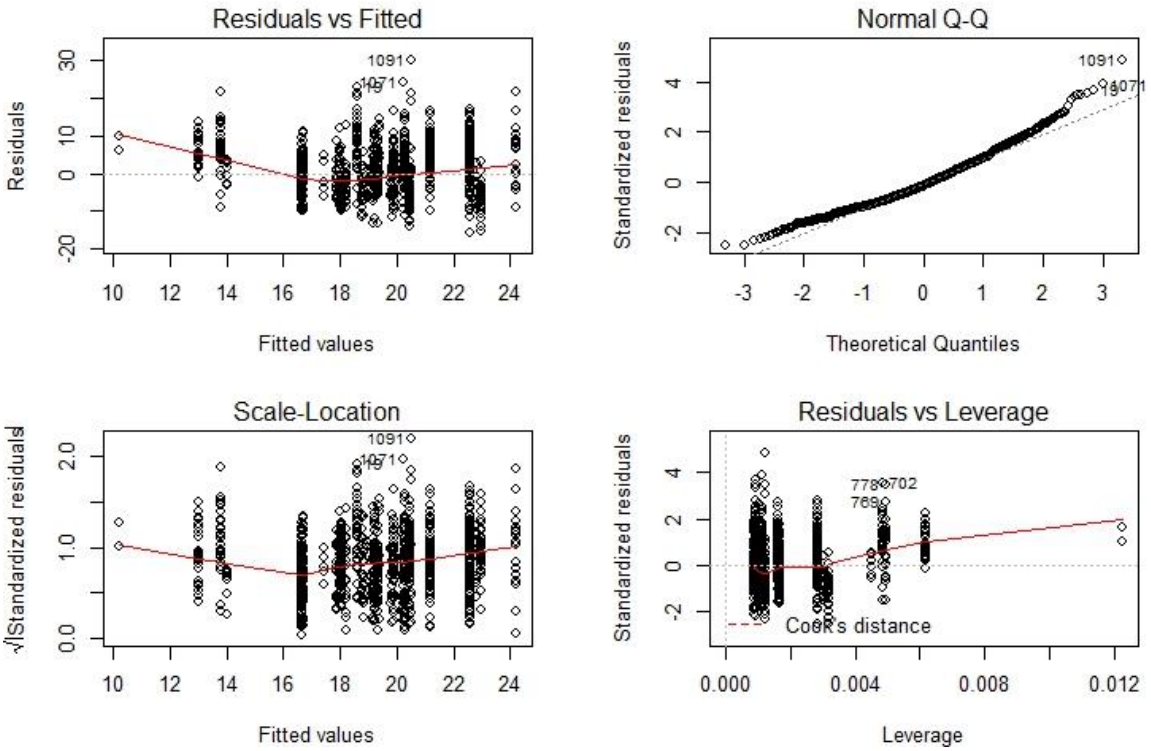

Figure A14. Plot of residuals from the analysis of Holmön. Age 4.

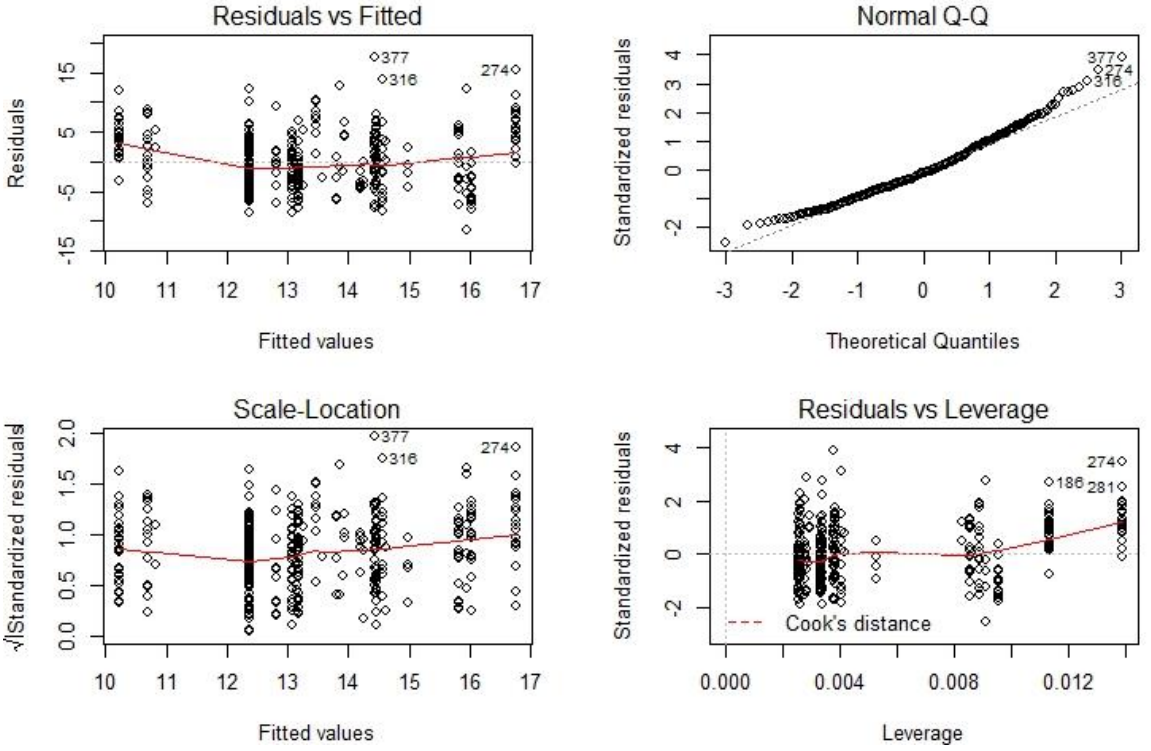

Figure A15. Plot of residuals from the analysis of Holmön. Age 5.

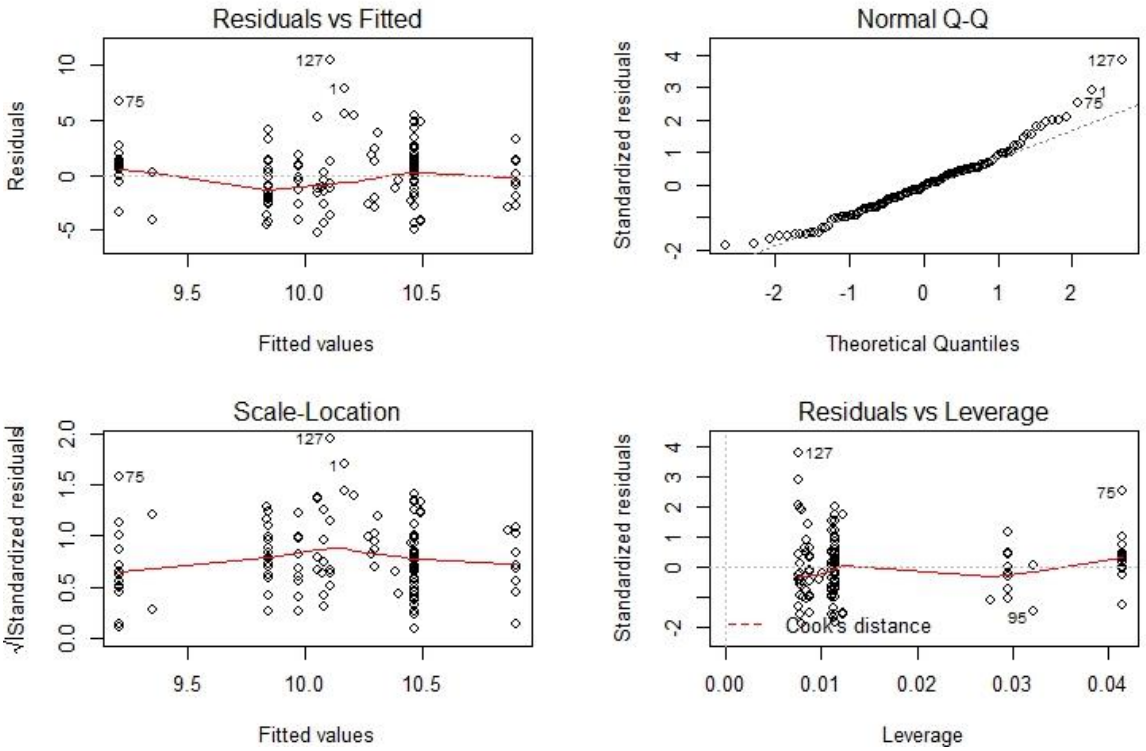

Figure A16. Plot of residuals from the analysis of Holmön. Age 6.

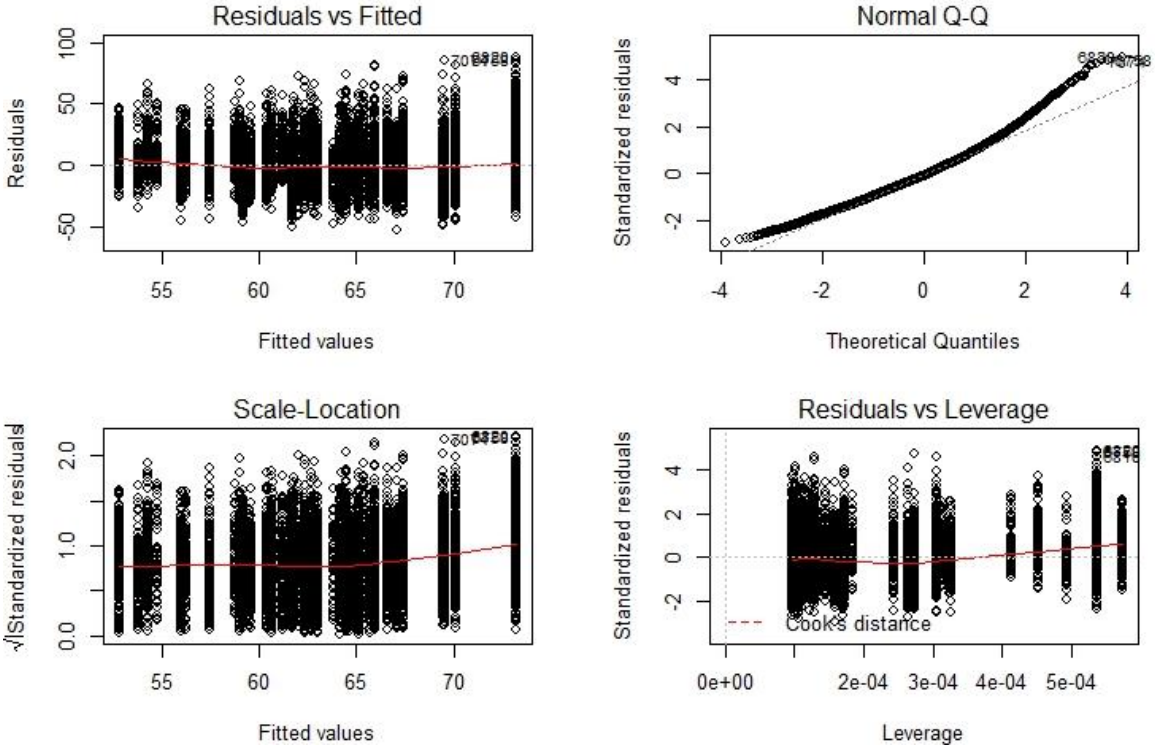

Figure A17. Plot of residuals from the analysis of Finbo. Age 1.

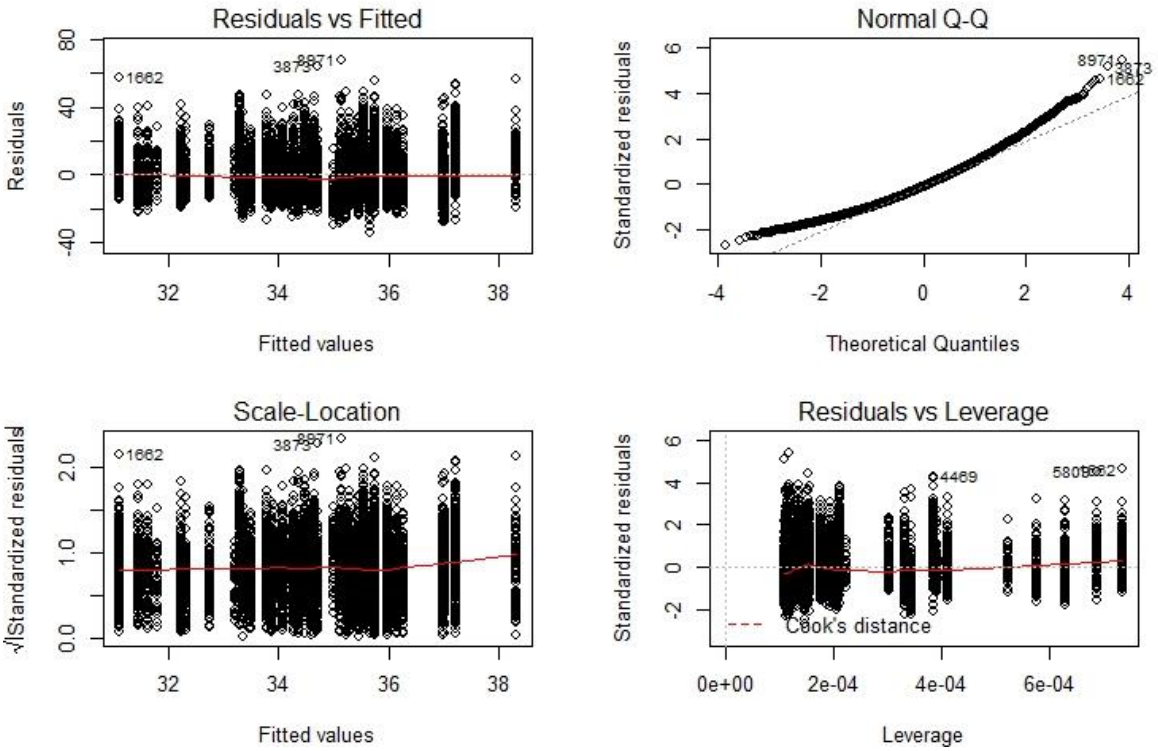

Figure A18. Plot of residuals from the analysis of Finbo. Age 2.

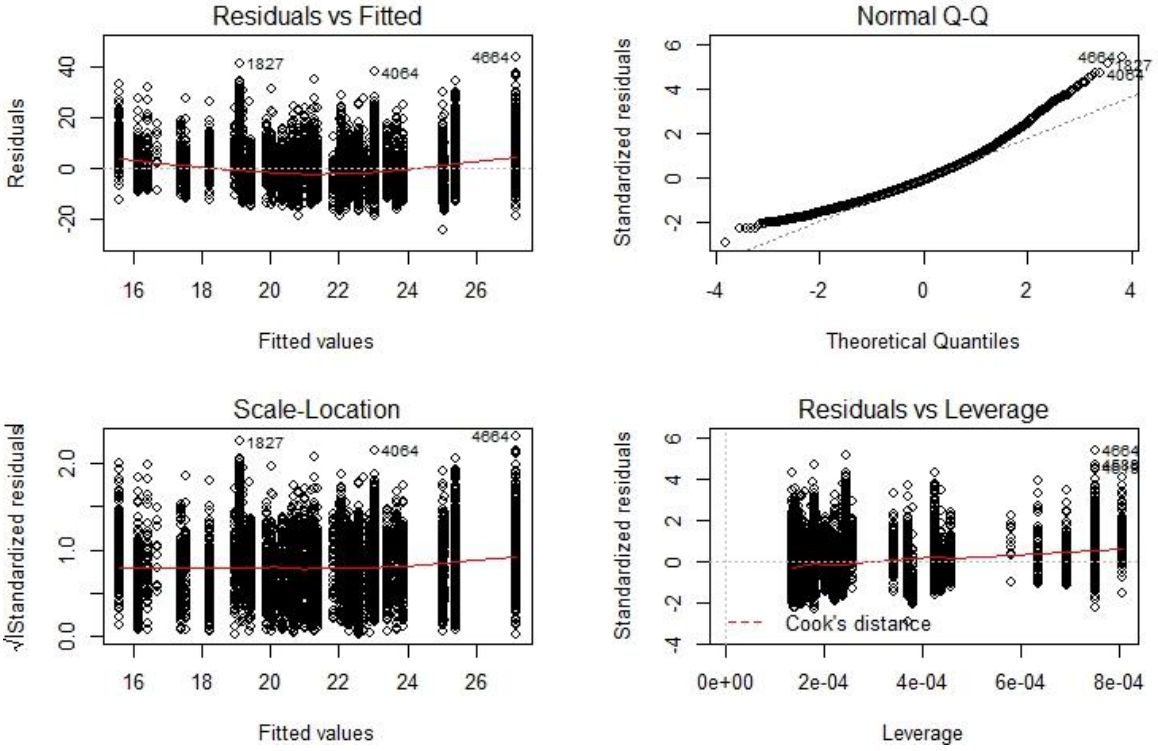

Figure A19. Plot of residuals from the analysis of Finbo. Age 3.

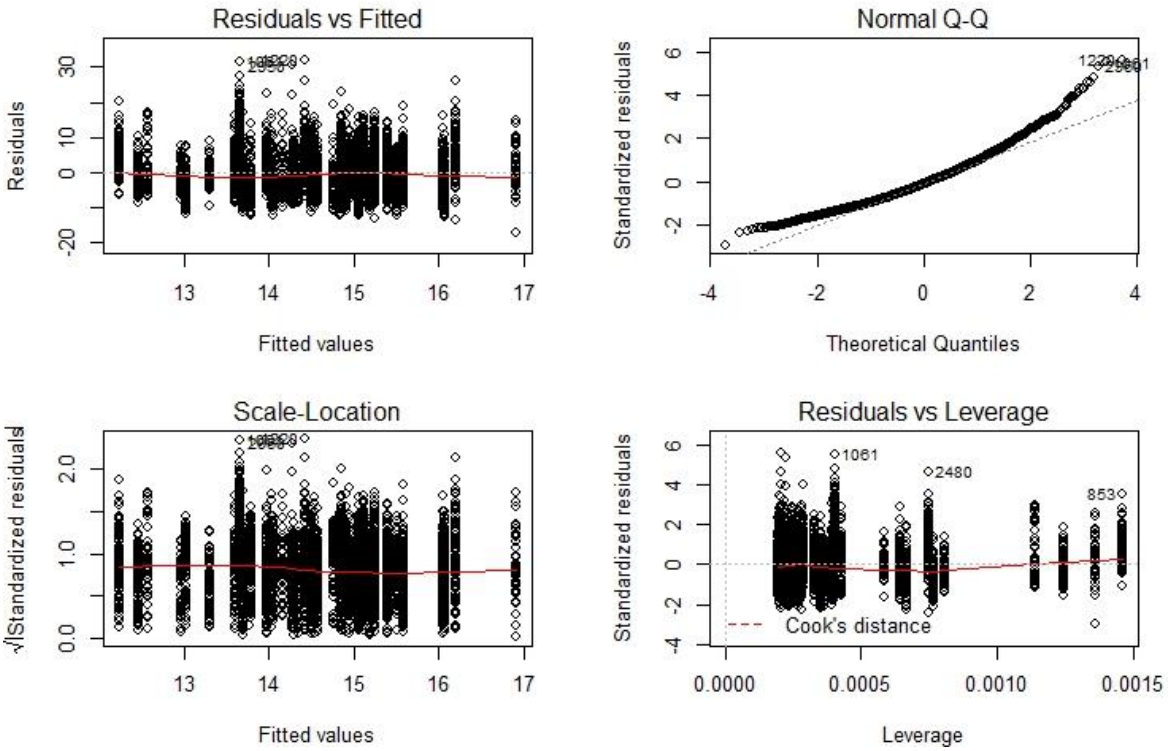

Figure A20. Plot of residuals from the analysis of Finbo. Age 4.

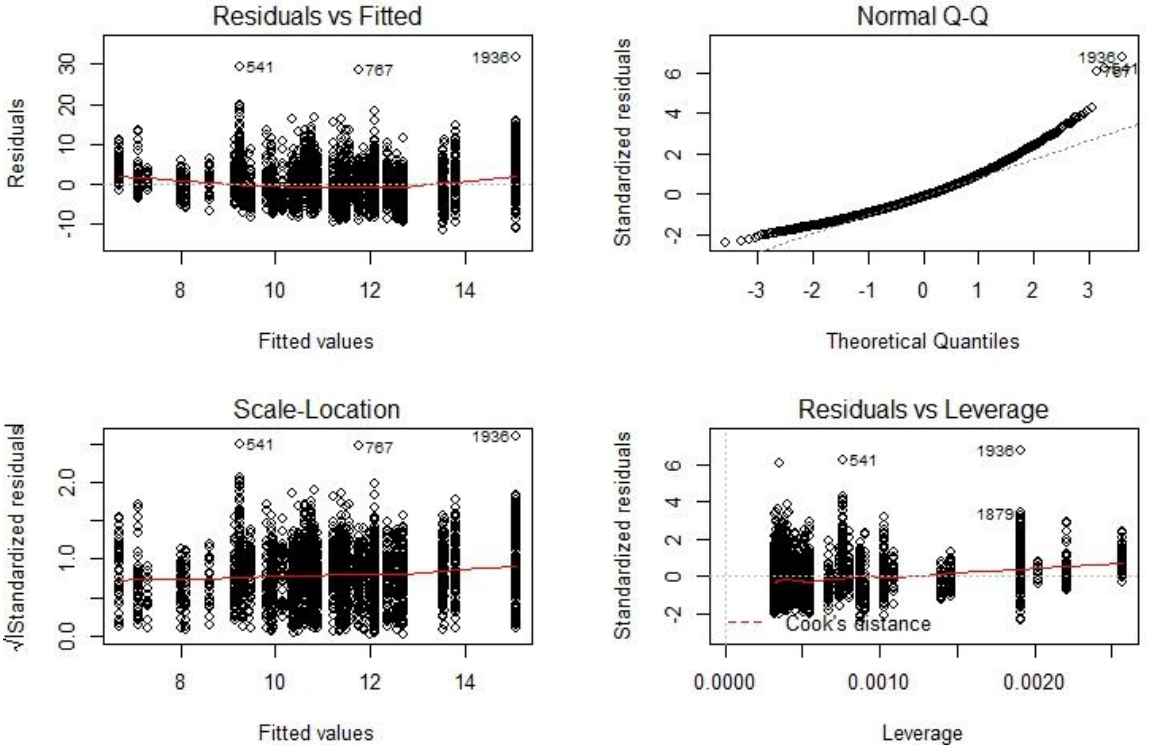

Figure A21. Plot of residuals from the analysis of Finbo. Age 5.

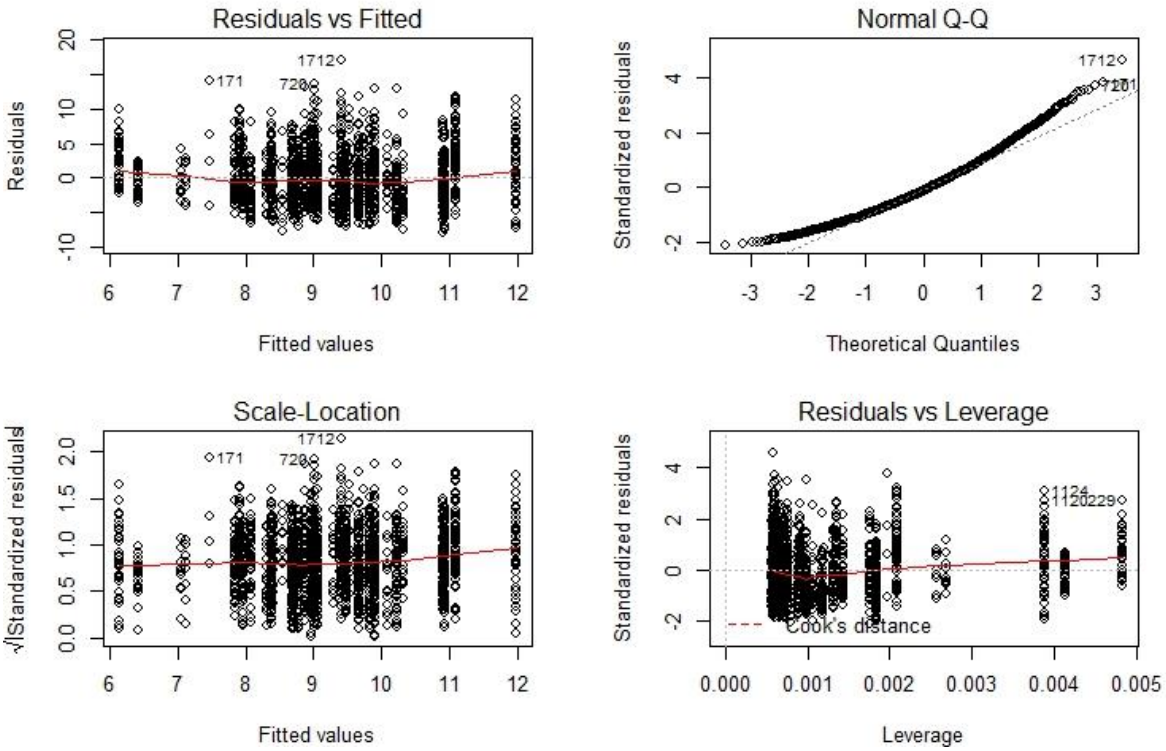

Figure A22. Plot of residuals from the analysis of Finbo. Age 6.

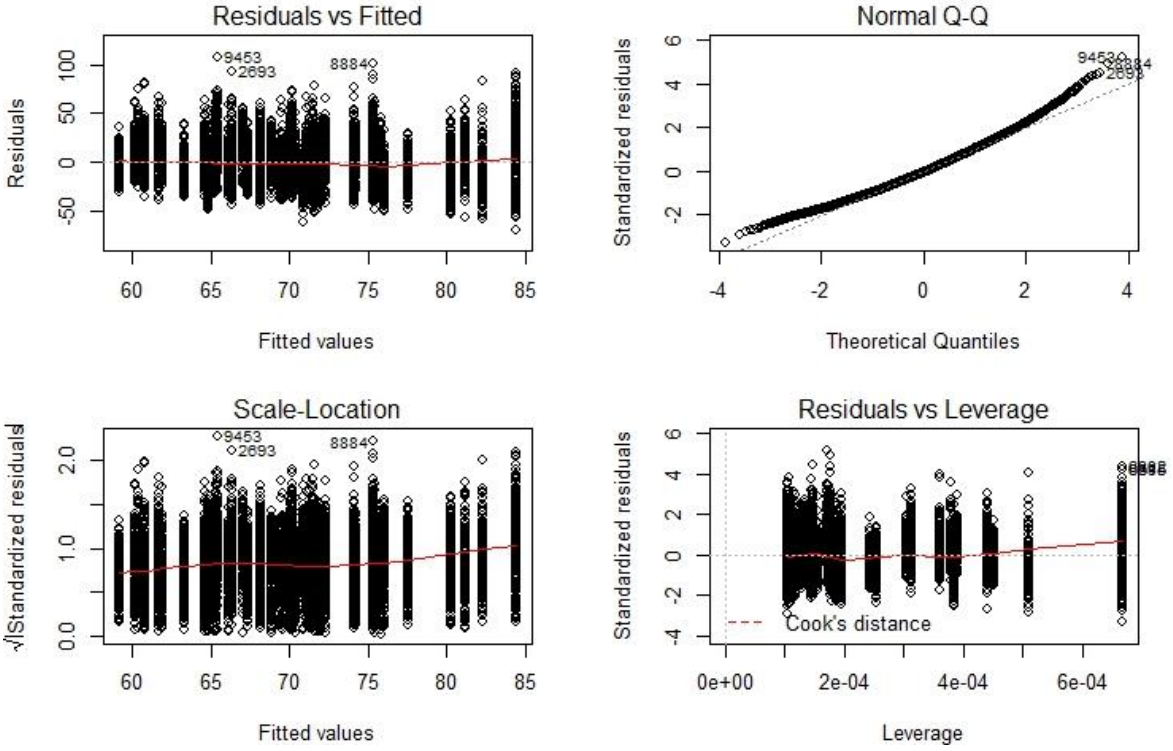

Figure A23. Plot of residuals from the analysis of Kvädöfjärden. Age 1.

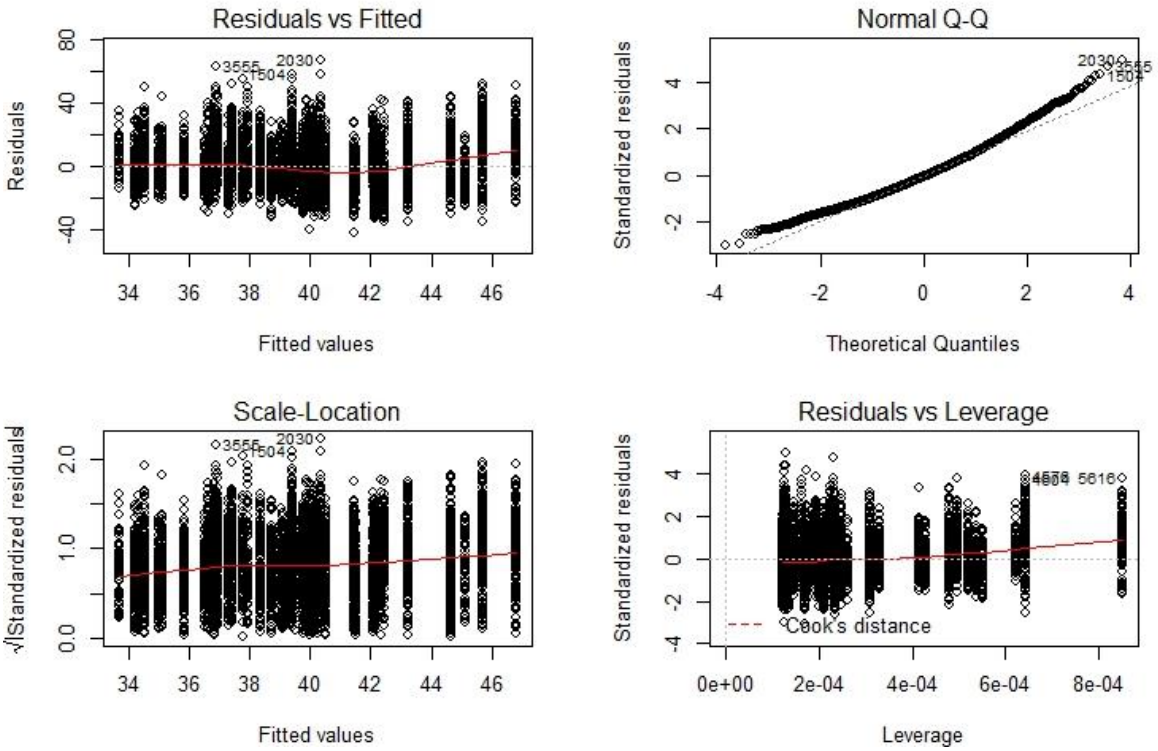

Figure A24. Plot of residuals from the analysis of Kvädöfjärden. Age 2.

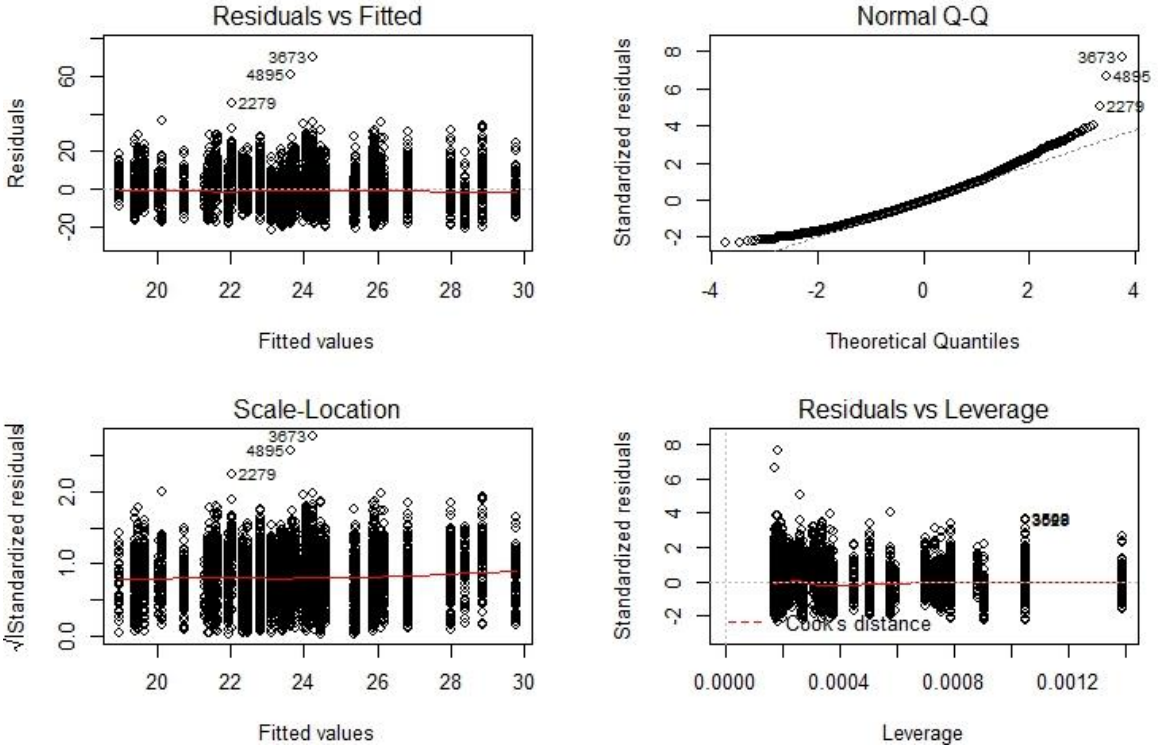

Figure A25. Plot of residuals from the analysis of Kvädöfjärden. Age 3.

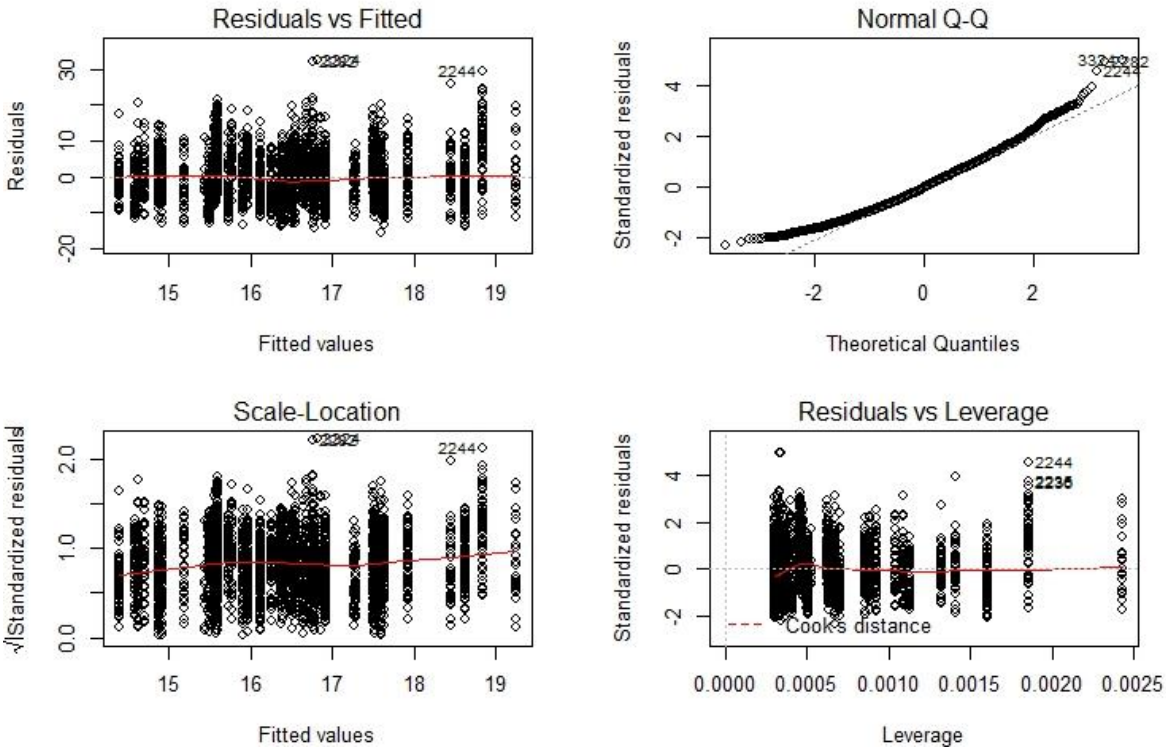

Figure A26. Plot of residuals from the analysis of Kvädöfjärden. Age 4.

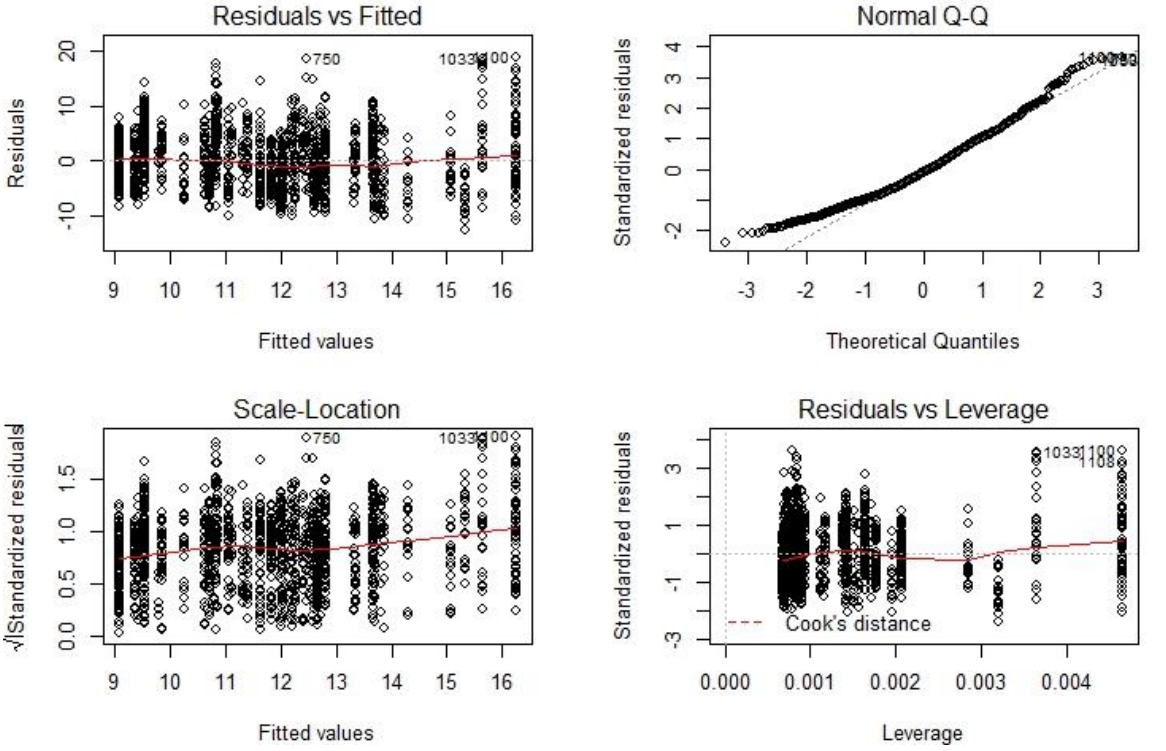

Figure A27. Plot of residuals from the analysis of Kvädöfjärden. Age 5.

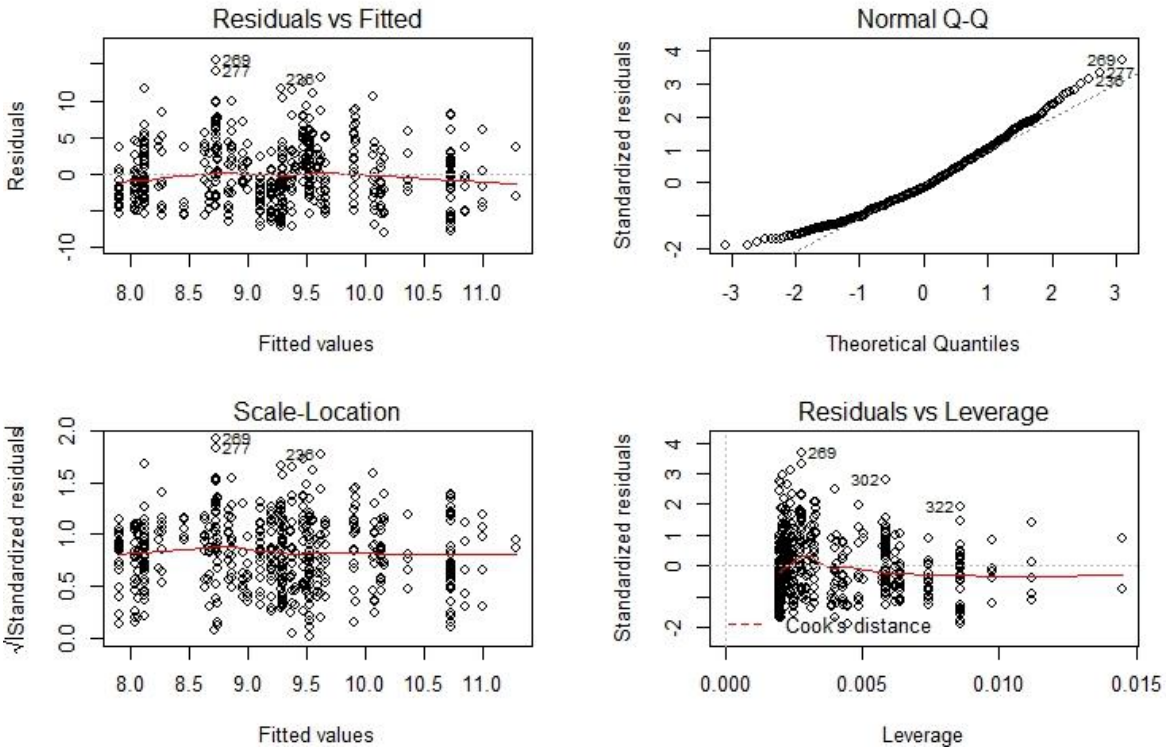

Figure A28. Plot of residuals from the analysis of Kvädöfjärden. Age 6.

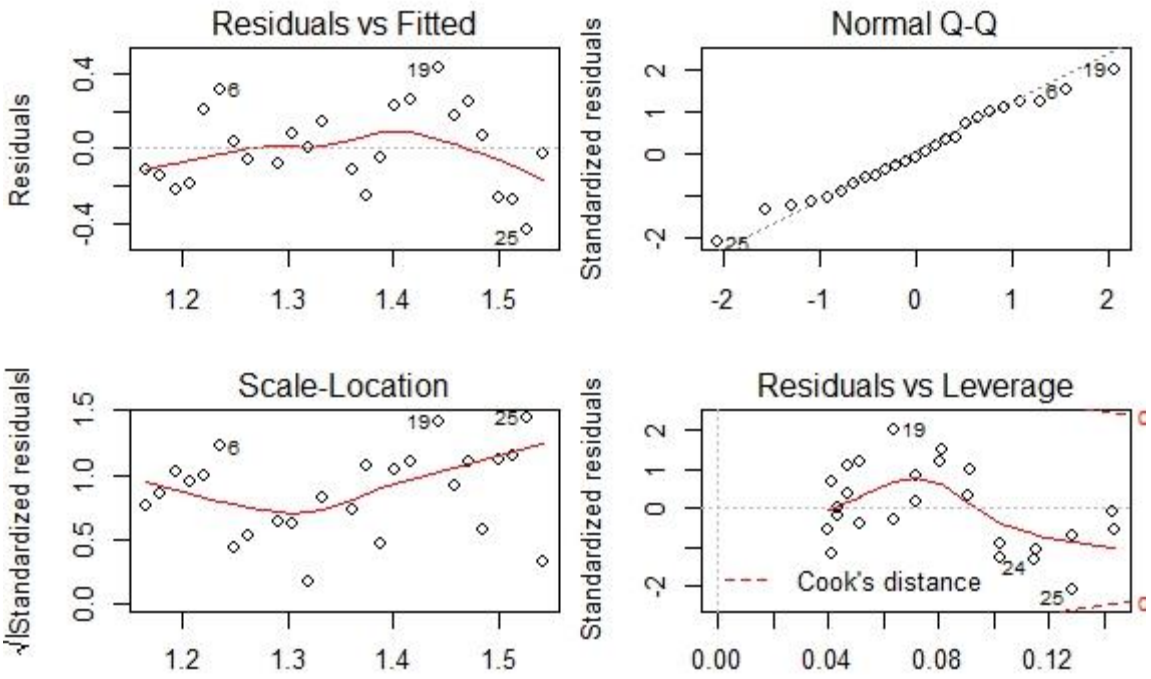

Figure A29. Plot of residuals from the analysis of Holmön, class 50 mm.

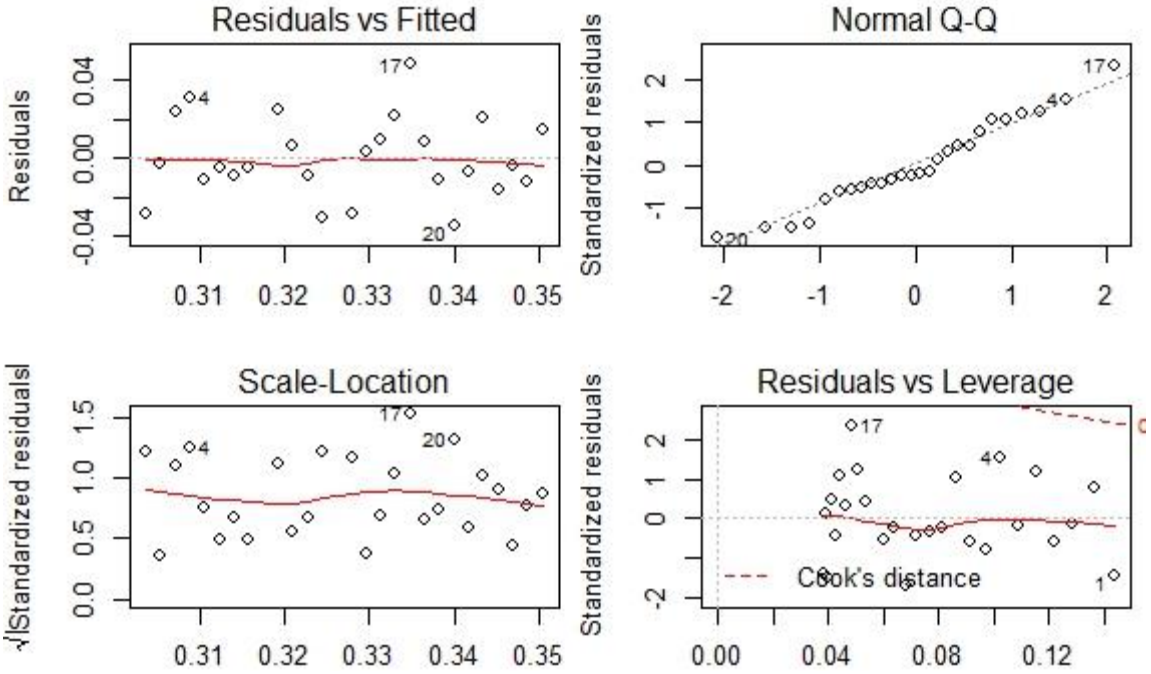

Figure A30. Plot of residuals from the analysis of Holmön, class 145 mm.

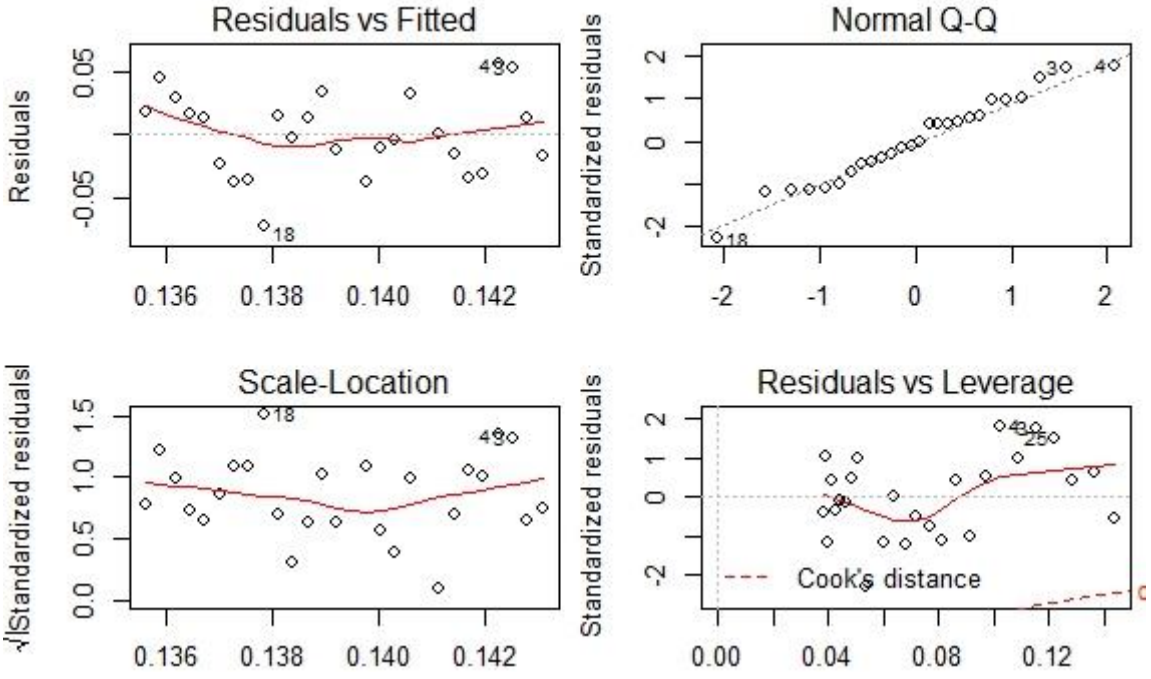

Figure A31. Plot of residuals from the analysis of Holmön, 240 mm.

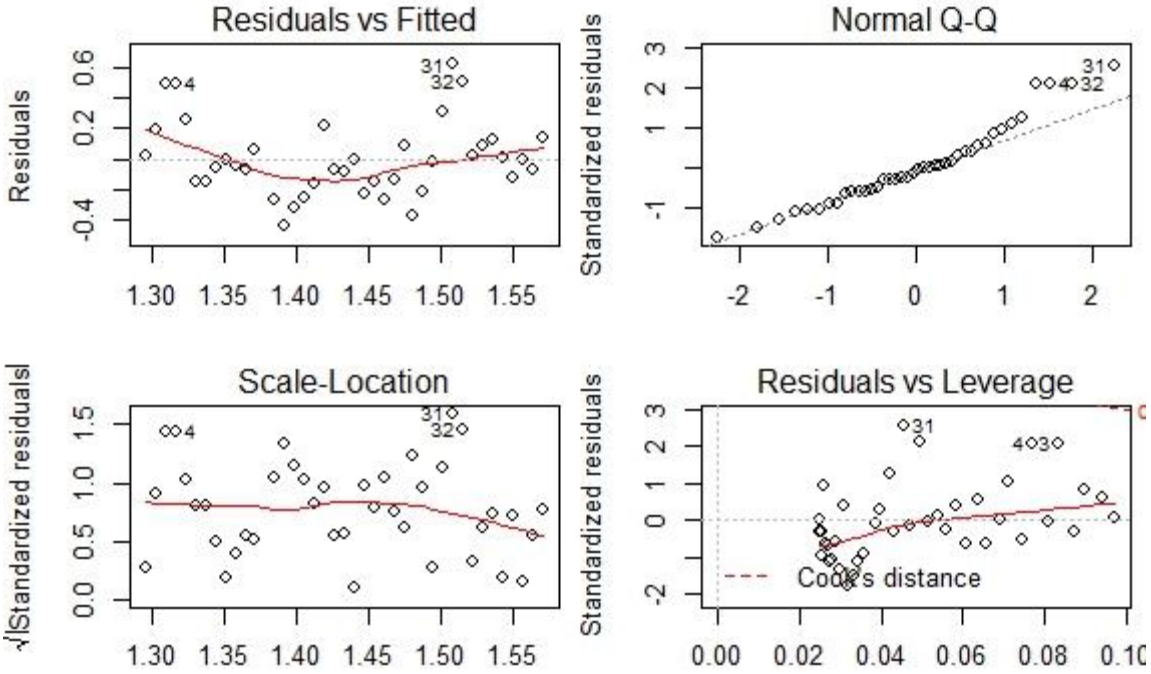

Figure A32. Plot of residuals from the analysis of Finbo, class 50 mm.

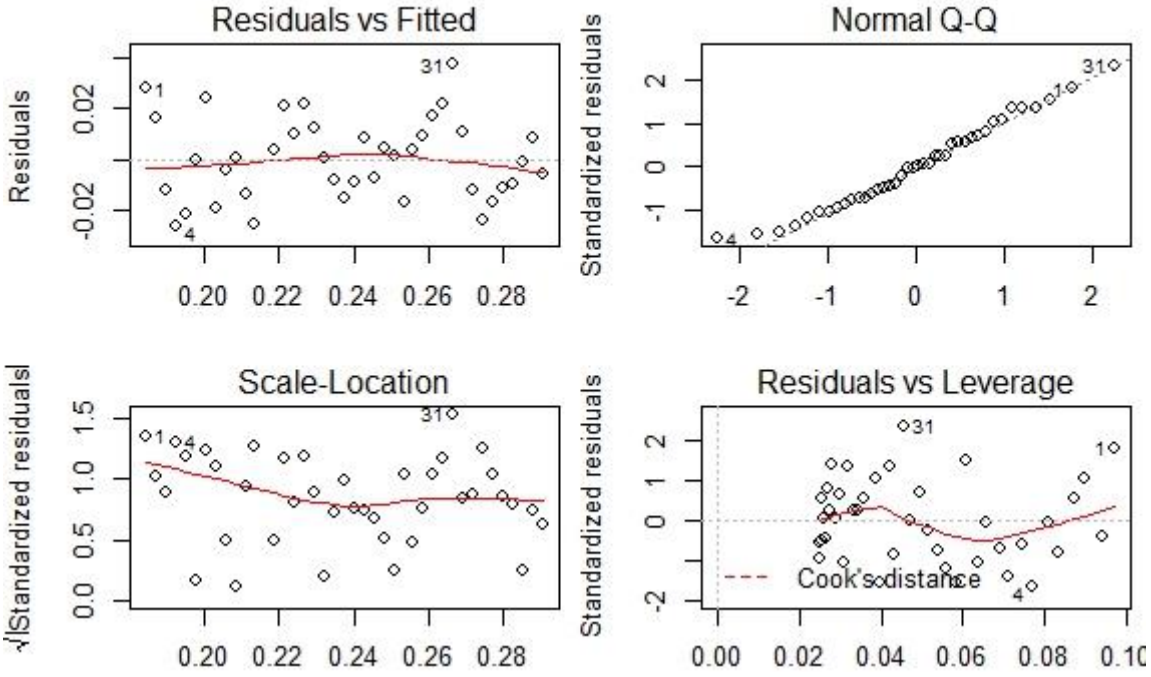

Figure A33. Plot of residuals from the analysis of Finbo, class 145 mm.

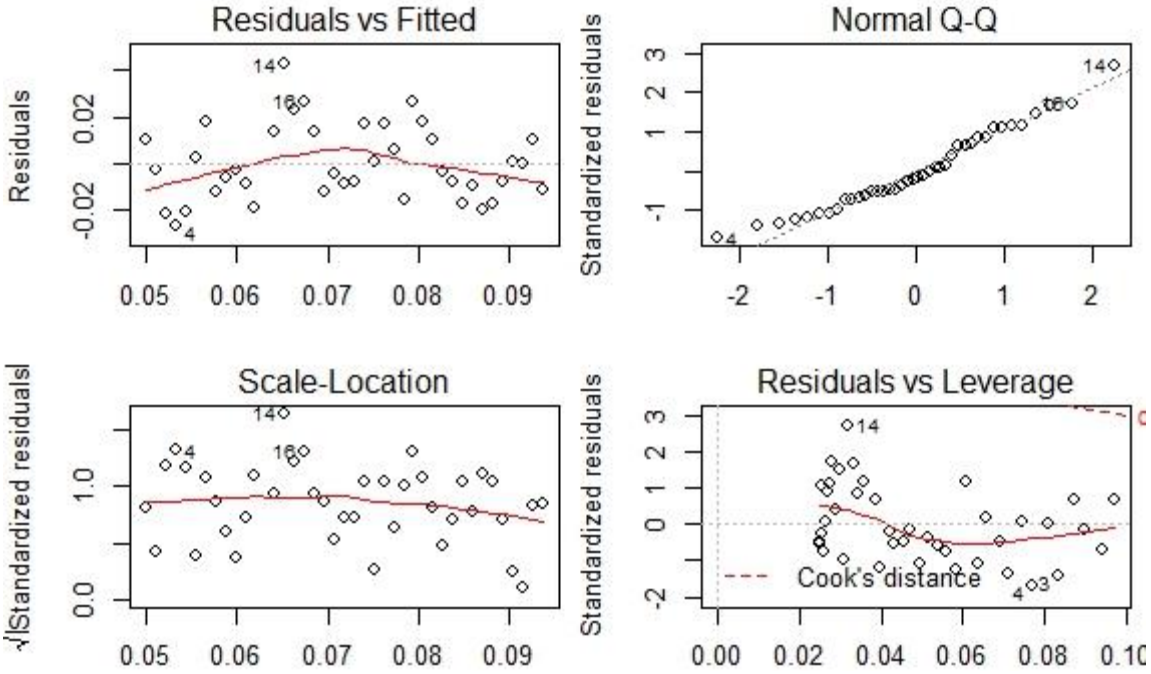

Figure A34. Plot of residuals from the analysis of Finbo, class 240 mm.

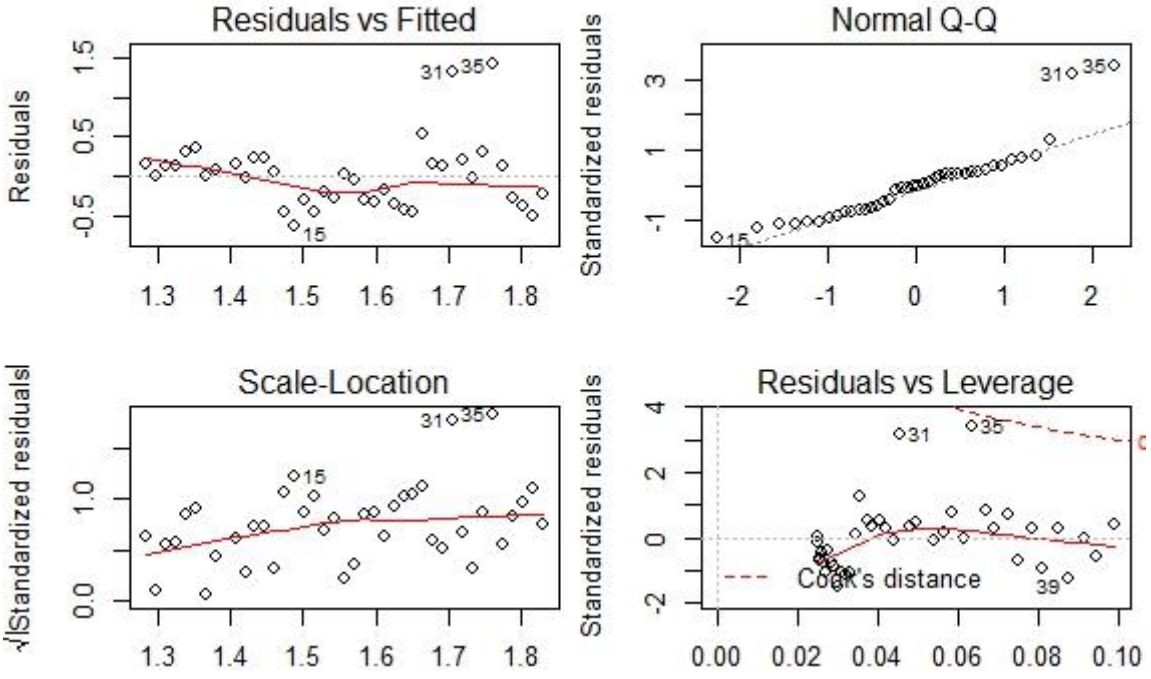

Figure A35. Plot of residuals from the analysis of Kvädöfjärden, class 50 mm.

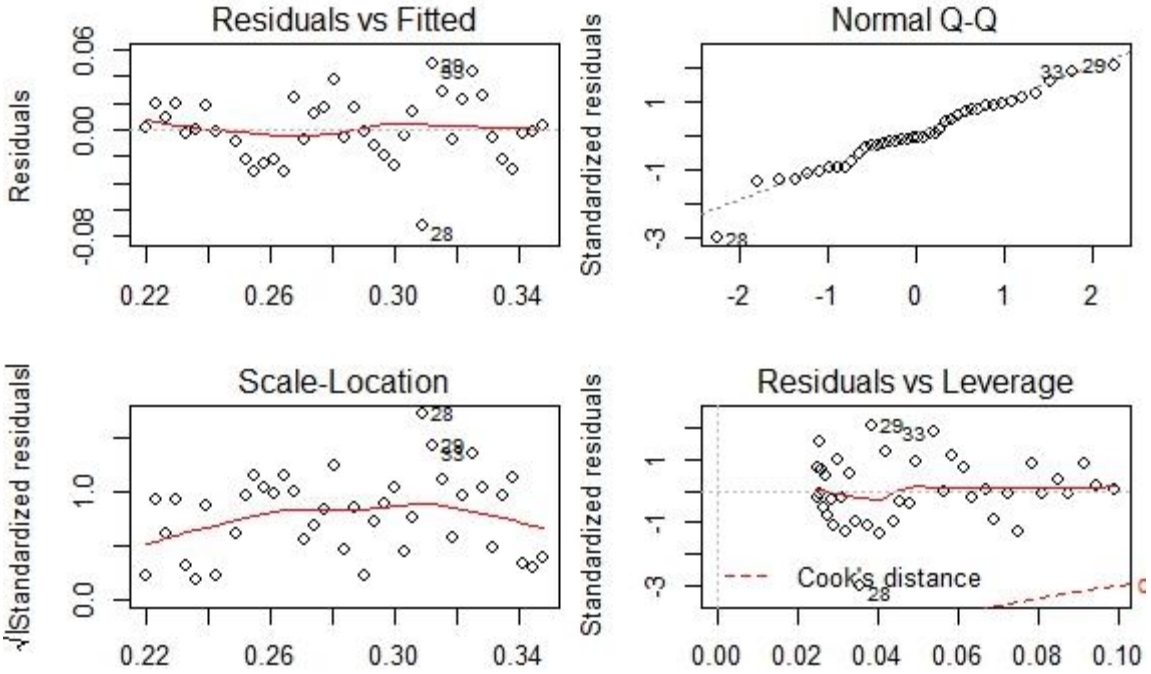

Figure A36. Plot of residuals from the analysis of Kvädöfjärden, class 145 mm.

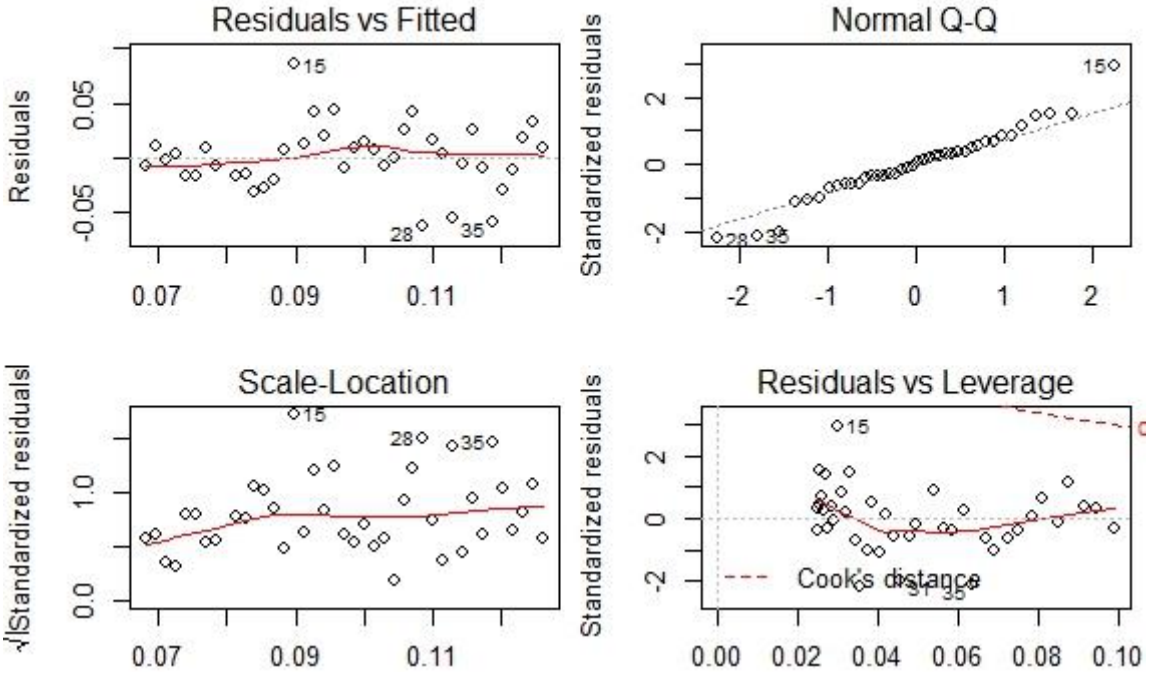

Figure A37. Plot of residuals from the analysis of Kvädöfjärden, class 240 mm.

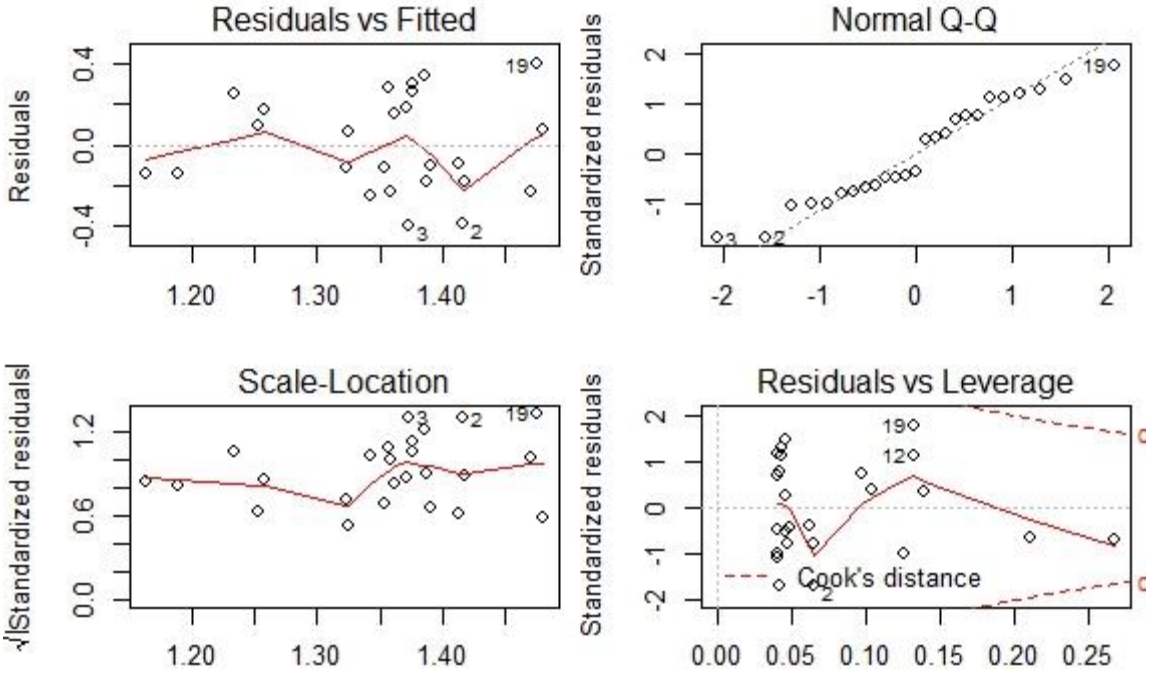

Figure A38. Plot of residuals from the analysis of Holmön, size class 50mm and temperature.

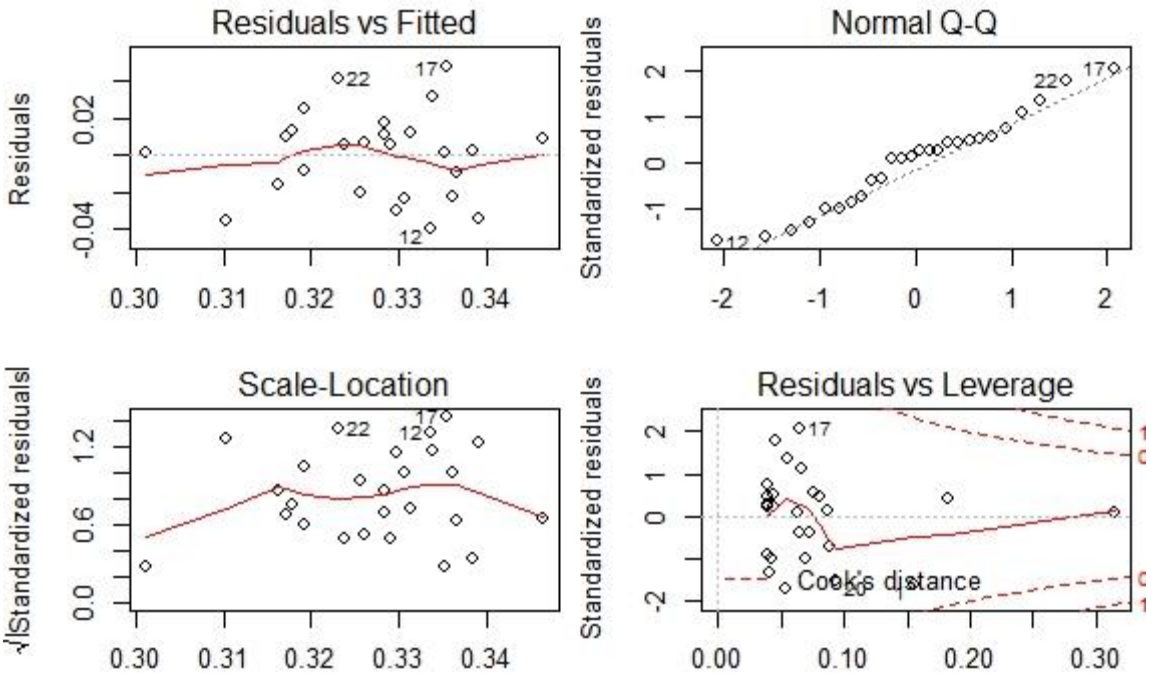

Figure A39. Plot of residuals from the analysis of Holmön, size class 145 mm and temperature.

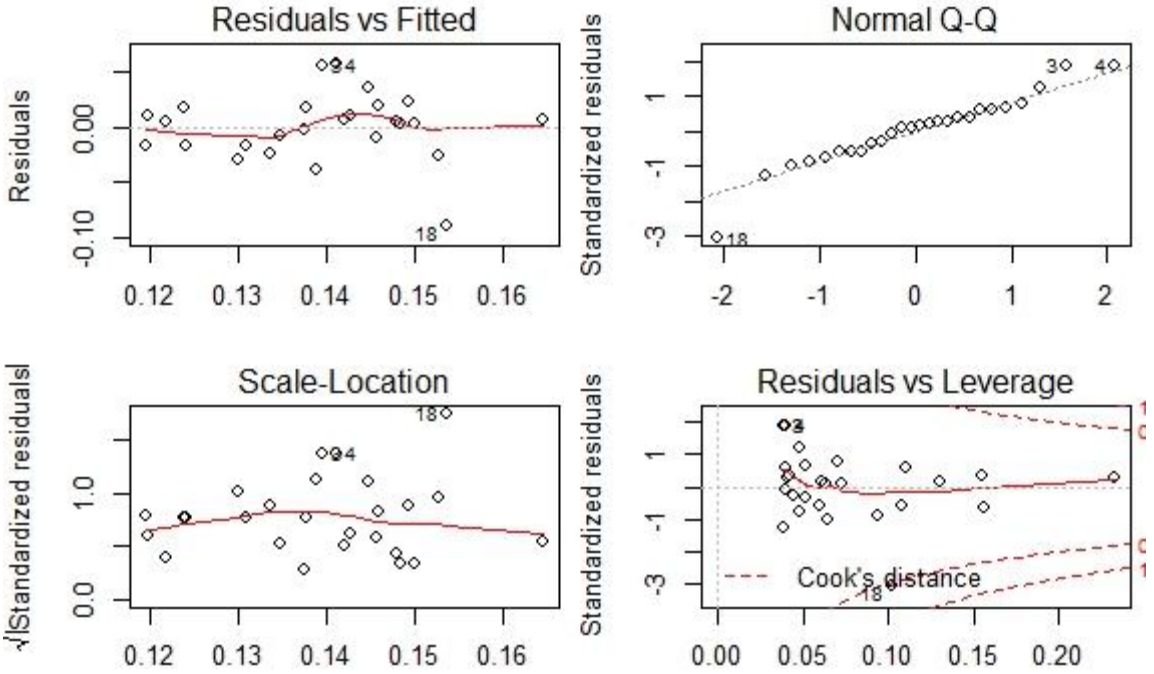

Figure A40. Plot of residuals from the analysis of Holmön, size class 240 mm and temperature.

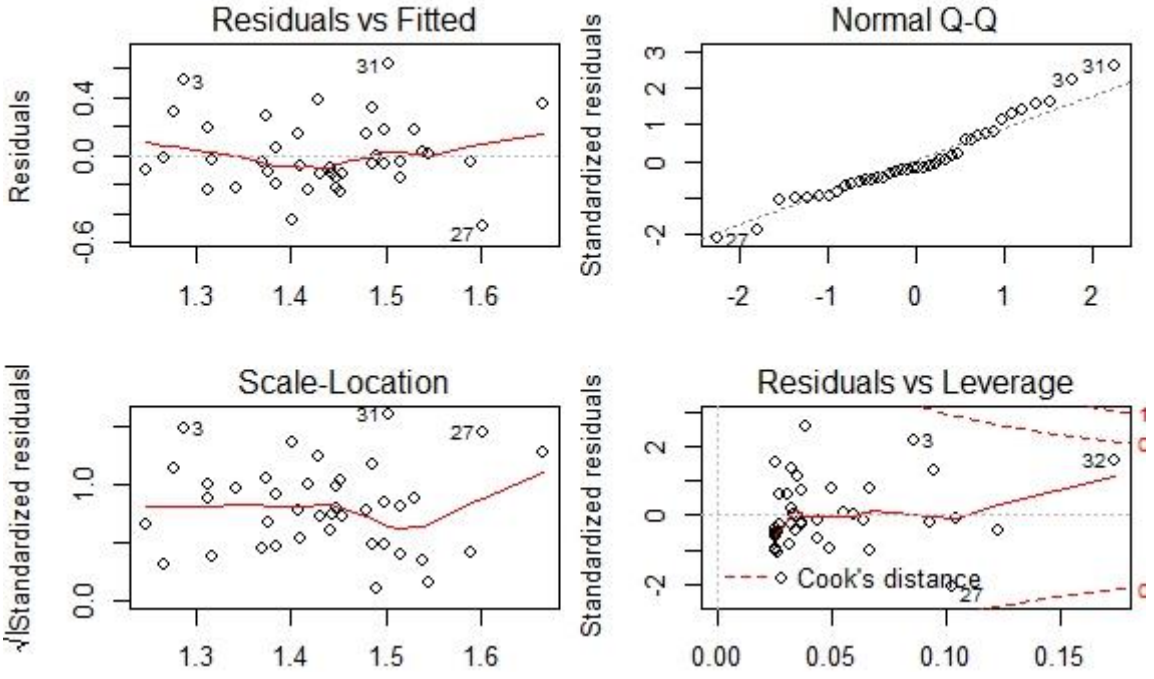

Figure A41. Plot of residuals from the analysis of Finbo, size class 50 mm and temperature.

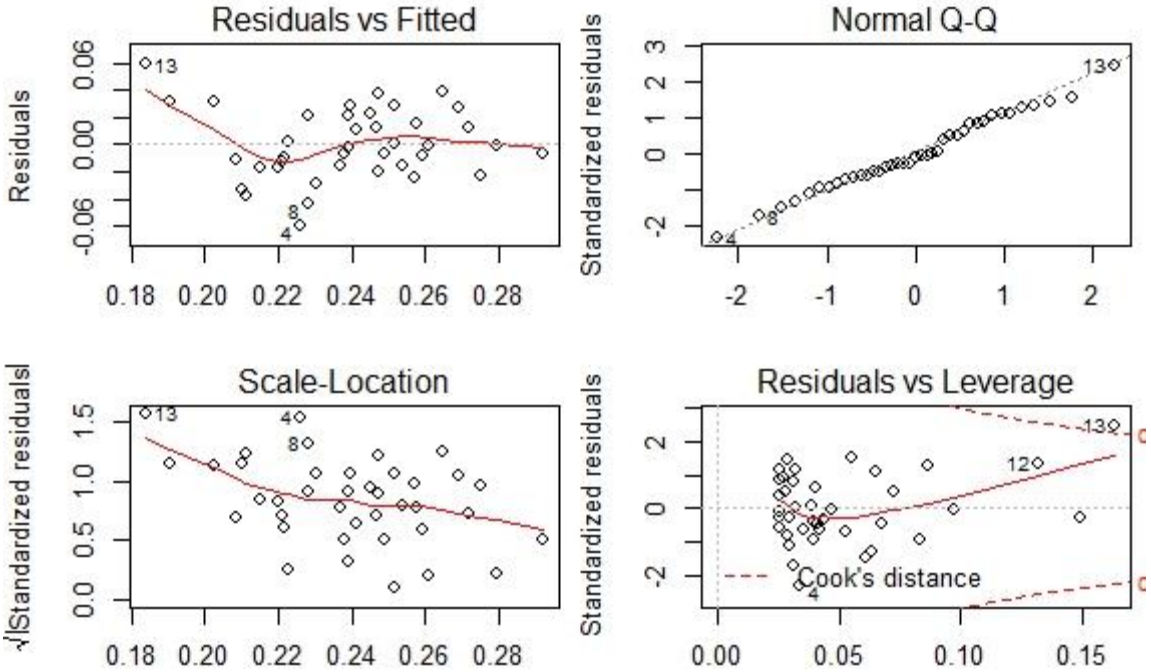

Figure A42. Plot of residuals from the analysis of Finbo, size class 145 mm and temperature.

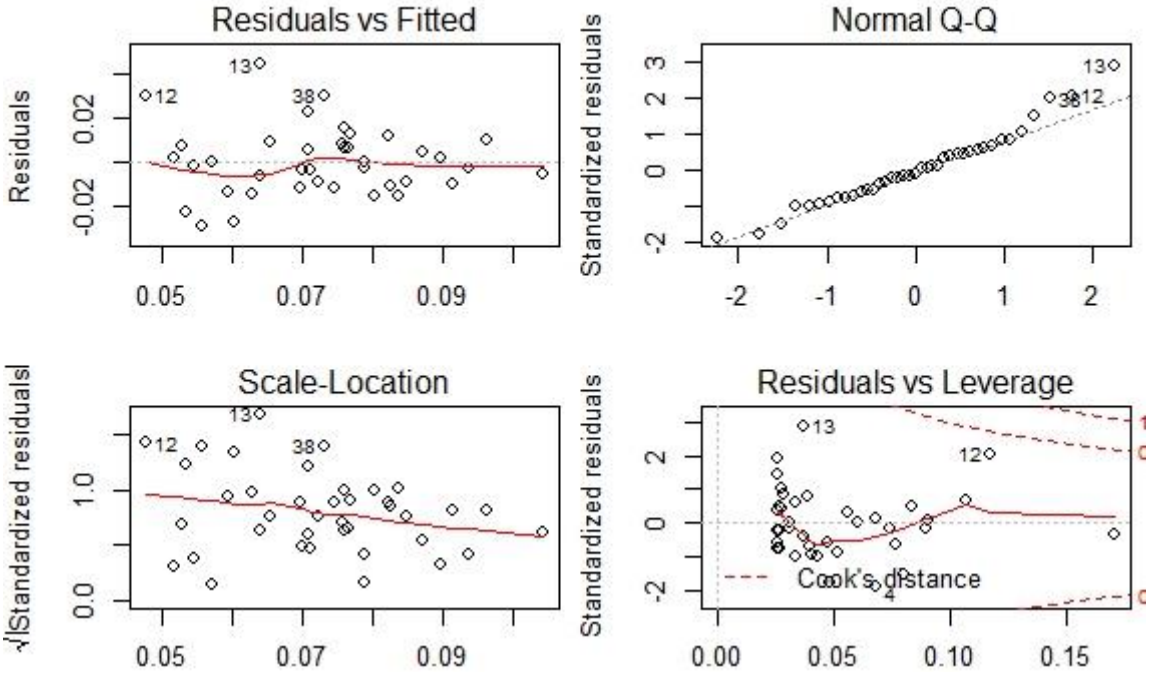

Figure A43. Plot of residuals from the analysis of Finbo, size class 240 mm and temperature.

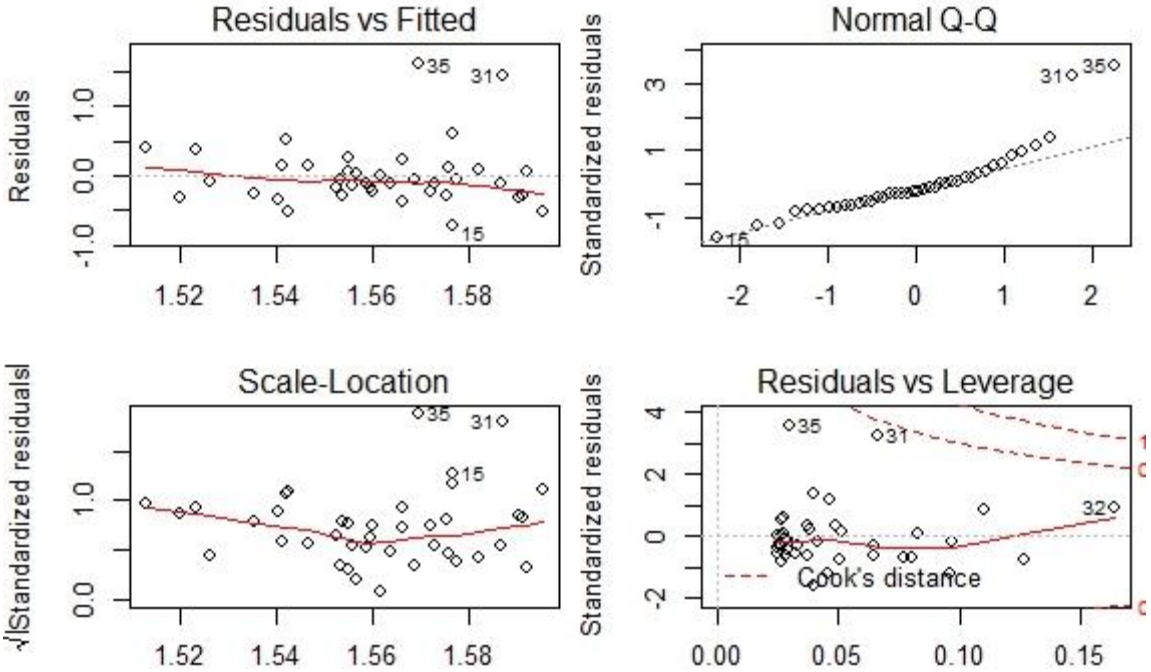

Figure A44. Plots of residuals from the analysis of Kvädöfjärden, size class 50 mm and temperature.

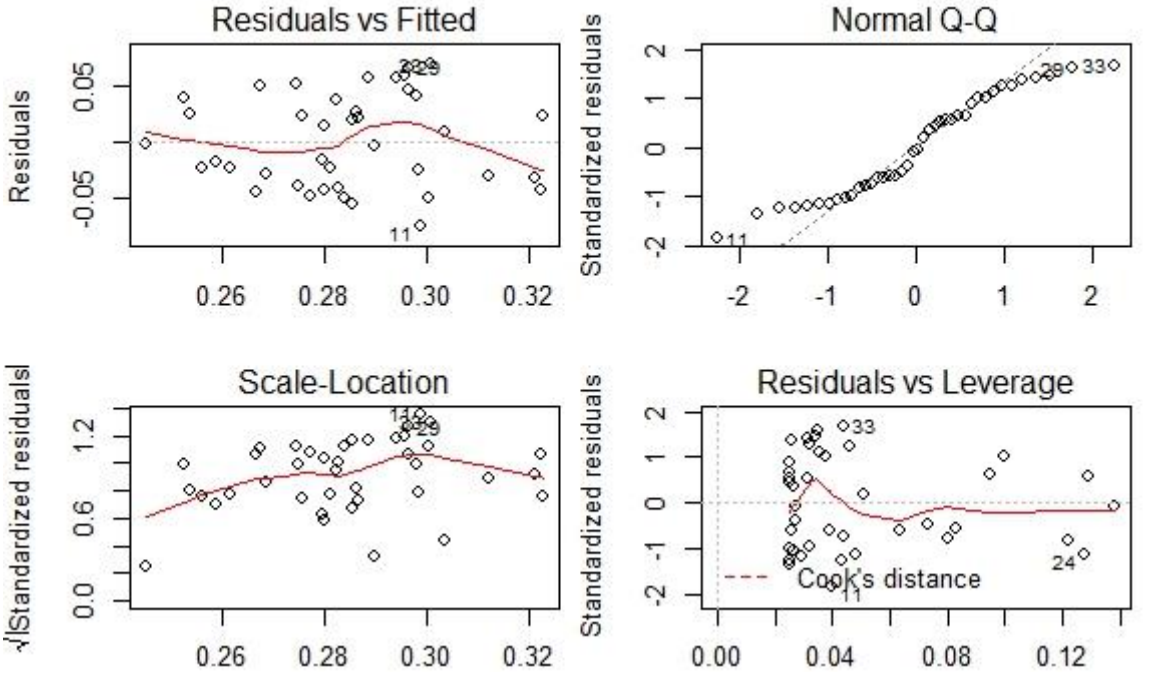

Figure A45. Plot of residuals from the analysis of Kvädöfjärden, size class 145 mm and temperature.

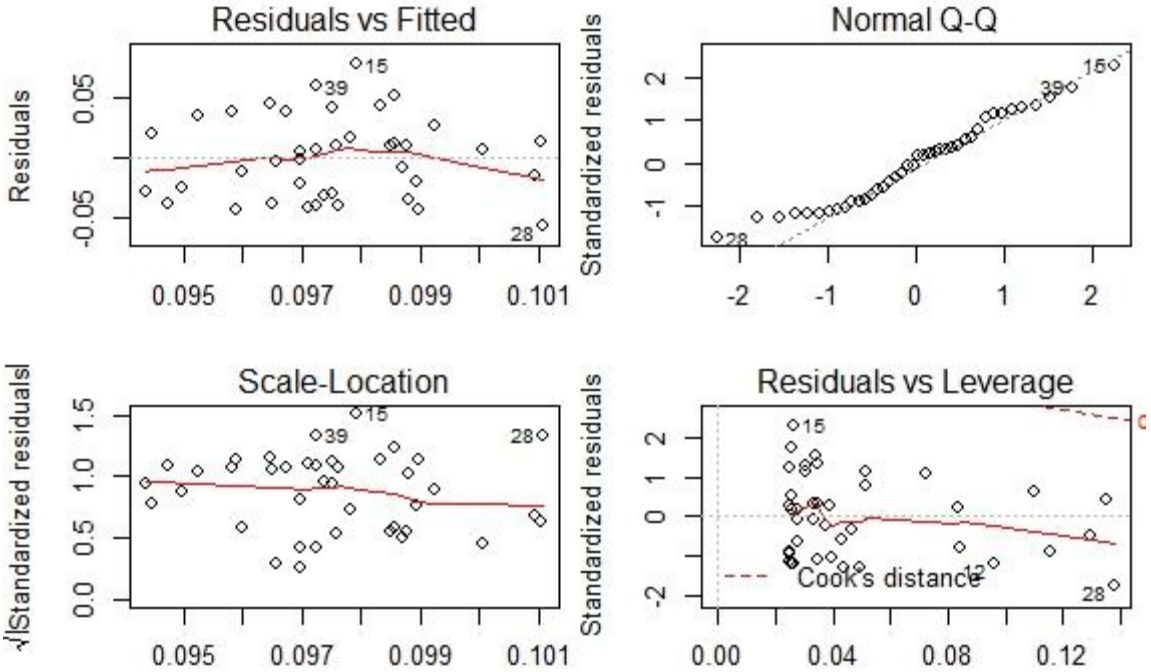

Figure A46. Plot of residuals from the analysis of Kvädöfjärden, size class 240 mm and temperature.